ECOLOGY

Vol. 37 OCTOBER, 1956 No. 4

A BIOLOGICAL TEST FOR DETERMINING THE POTENTIAL PRODUCTIVITY OF WATER[1]

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INTRODUCTION

Estimates of potential phytoplankton production in natural waters are usually based on chemical assay of nitrogen and phosphorus compounds. While chemical analysis yields information on the quantity of nutrients present, it supplies no knowledge of their availability for phytoplankton utilization. Only through the application of biological assay methods can such information be obtained.

Schreiber (1927) followed such an approach when he used pure algal cultures to assay the nutrients available in sea water. Strøm (1933) applied the Schreiber method to fresh water and suggested that the technique could prove an effective means of estimating utilizable nutritive salt content.

The present study applies a modification of the Schreiber method to the seasonal study of nutrients in two farm ponds. The green alga *Kirchneriella subsolitaria* G. S. West was found to be a suitable assay organism.

The author is deeply indebted to Dr. L. C. Cole for his helpful advice and direction throughout the course of this project. The constructive criticisms of Dr. D. C. Chandler are also gratefully acknowledged.

PONDS STUDIED

A study was made of two artificial farm ponds located near Ithaca, New York. The larger pond, called Upper Pond, covers about two acres and was constructed in the spring of 1950. About one-fourth of a mile from Upper Pond is a smaller pond, termed Lower Pond, approximately one-and-a-half acres in size and two years older than Upper Pond. This difference in age was reflected by the nature of the shorelines. Upper Pond had no shore growth, the muddy bank extending several feet beyond the water-line. The bottom was muddy, with no visible aquatic plants. Lower Pond had a dense shore growth, and a bottom covered by submerged rooted aquatics and filamentous algae.

Upper Pond receives its water from two irrigation ditches which drain the surrounding fields. These fields are cultivated and are fertilized from time to time. A constant water level is maintained by means of an overflow outlet. The overflow from Upper Pond passes within twenty feet of Lower Pond, but does not drain into it. Lower Pond is supplied entirely by precipitation and seepage, which are ample to maintain a relatively constant water level. Both ponds have a maximum depth of approximately two meters.

MATERIALS AND METHODS

This study was conducted from November 3, 1950, to August 10, 1951. Samples of water for the laboratory tests were collected from each of the ponds at intervals spaced so as to permit evaluation of the seasonal changes. Water samples were taken with the aid of a 2-liter Kemmerer water sampler. On Lower Pond, five stations were established and at each station a sample was taken from the upper meter of water. These samples were then emptied into a five-gallon water can, yielding a composite sample (Chandler and Weeks 1945). Lack of a boat precluded use of this method on Upper Pond. One station was established at the end of a pier extending about three meters from the shore. One sample was taken by lowering a five-gallon water can about one-third of a meter below the surface. When necessary, the samples were collected through holes cut in the ice cover.

The water samples were filtered, first through ignited white silica sand, and then through a

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[1] Revision of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Cornell University, Ithaca, New York.

Seitz bacteriological filter. Controls indicated that this procedure removed all plankton. There was no cloudiness or other abnormality that could be attributed to bacterial growth.

Upon completing the filtering process, six 500-cc samples from each pond were placed in quart fruit jars. One sample from each pond was designated as a control. To one sample from each pond was added four drops of Na_2Co_3 solution; to another from each pond, four drops of $Ca(No_3)_2$ solution; to another, KH_2PO_4; to another $MgSO_4$; and to the sixth sample from each pond was added four drops of each of the four nutrient solutions. It has been found (L. C. Cole, unpublished data) that these inorganic substances, in the amounts used (Table I), and in the degree of purity designated as "reagent" grade, when added to the purest distilled water, supply all essential nutrients for growth of *Kirchneriella subsolitaria* G. S. West, the alga used as an index organism in this study. The strain used was originally isolated from the digestive tract of a cladoceran by Dr. L. C. Cole.

TABLE I. Quantities and concentrations of inorganic nutrients used

Nutrient	Stock solution in gm/liter	µg added/cc of sample (4 drops)	µg anion added/mm^3 of sample (4 drops)
$Na_2CO_3.H_2O$	7.0	2.544	.001231
$Ca(NO_3)_2$	12.2	4.440	.003357
KH_2PO_4	12.2	4.240	.002962
$MgSO_4$	18.0	7.200	.005760

To each sample was added an inoculum of approximately 100,000 cells of *K. subsolitaria* suspended in one ml of water. All samples were inoculated from subcultures 10-12 days old, the period during which the maximum rate of growth was obtained, under the conditions of this experiment.

After inoculation the samples were placed in a constant temperature room at 18.5° C. A constant light source was supplied by a fixture containing two 20-watt fluorescent tubes located one meter above the glass jar tops, and arranged so that light of equal intensity was supplied to all samples.

Population density was determined by the direct cell count method. This technique was preferred to the less time-consuming extraction and colorimetric methods, because the quantitative reliability of the latter methods is still questioned (*e.g.* Juday, Blair and Wilda 1943; Rodhe 1948; Pennak 1949; Tucker 1949).

Each sample was thoroughly mixed for thirty seconds, using a rubber squeeze bulb and glass tubing. One milliliter was then removed and placed in a Sedgwick-Rafter counting chamber. Application of the Poisson function to counts of *K. subsolitaria* indicated a random distribution of algal cells within the chamber, justifying its use during this study.

An 8-mm objective and 15X ocular containing a Howard ocular micrometer disc were employed in counting 20 randomly selected fields of the Sedgwick-Rafter cell. Daily counts were begun when growth became observable and continued until after maximum growth was obtained, a period of 10-12 days.

Population growth was treated statistically by application of the logistic function, which was found to approximate very closely the actual population increase of *K. subsolitaria*. Other mathematical expressions of population growth have been advocated (for examples, see Brody 1945). The logistic, however, gives an excellent representation of the data in this study and it is the most used growth function (Allee *et al.* 1949).

Several methods of fitting the logistic have been proposed (*e.g.* Pearl 1930). The method proposed by Berkson (1944) in connection with the application of the logistic function to bio-assay has been found adaptable to population growth problems, giving completely objective values for the constants. In this method minimum Chi-square is employed as the criterion of the best-fitting logistic curve. Others (Finney 1947a, 1947b) prefer the maximum likelihood estimate. Berkson (1949, 1951) finds the minimum Chi-square method to be quicker and to have smaller sampling error than the maximum likelihood estimates.

Berkson, in applying the logistic function to bio-assay data, determined dosage-mortality. In this application the upper limit is already determined, being 100% mortality. In the application of the logistic function to population growth problems, however, the upper asymptote, designated as *K*, is not fixed, but varies with different populations and with environmental conditions. Therefore, the procedure for obtaining the best-fitting curve was modified in the present study.

A value of *K* was chosen, and the actual cell counts were converted to percentages of the total population realized at the time of each count. These percentages were plotted on logistic graph paper (designed by Berkson and obtained from the Codex Book Co. Paper No. 32.450). Several other values of *K* were treated in the same manner until a *K* was found whose percentages came

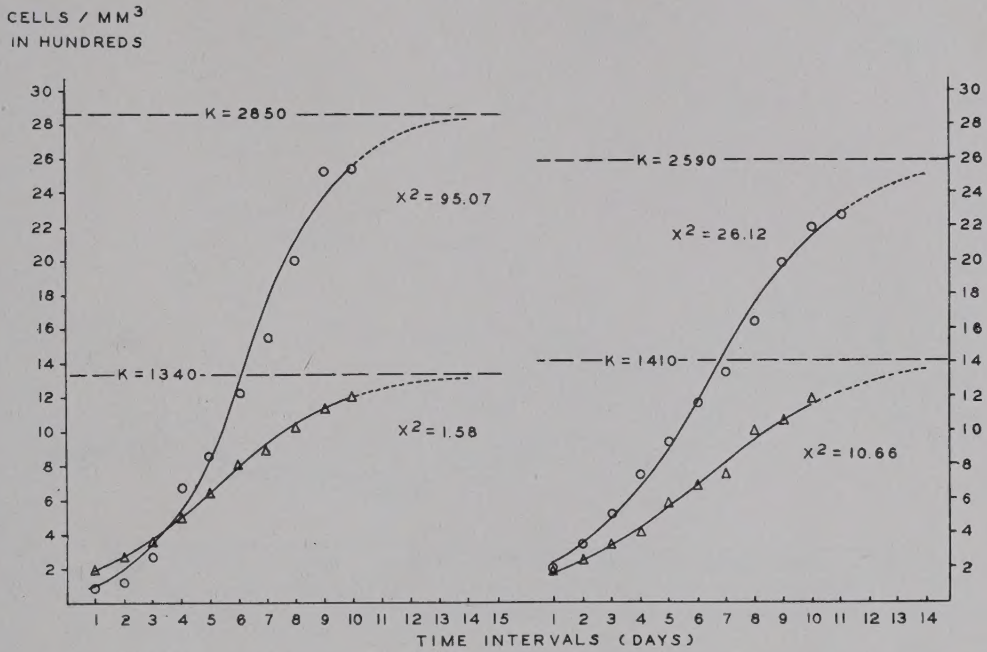

FIG. 1. Examples of logistic curves. The circles and triangles represent actual cell counts. The solid lines are the fitted logistics. The broken lines are the continuations of the calculated curves toward their upper asymptotes.

closest to forming a straight line when plotted on logistic paper. In choosing values for *K*, the figure was rounded off to the nearest ten (*i.e.*, 2150, 2160, 2170, etc.). The best-fitting logistic for this value of *K* was calculated by Berkson's method (1944), and its Chi-square computed.

A slightly higher *K* was then chosen and its Chi-square computed. This process was continued until the minimum Chi-square value was obtained, that value of *K* being considered the upper asymptote of growth for the algal population in question.

Several samples of logistic curves are presented in Figure 1. Those plotted on the left signify the best-fitting and the worst-fitting curves obtained during the course of this study, as indicated by the low Chi-square value of 1.58 and the high Chi-square value of 95.07 respectively. Even in the latter case actual cell counts do not deviate greatly from the calculated curve. It might be pointed out that the points nearer the lower asymptote, representing counts made during the early phase of growth, have a greater influence on the Chi-square value, and are also more subject to experimental error.

The curves plotted on the right are examples of how the results were used in the present study. Taken from a water sample of the same day, the lower curve, with a *K*-value of 1410 cells per mm³, was the control sample. The total amount of growth supported is a quantitative indication of the nutrients present in the original sample. The upper curve represents the same water with four drops of $Ca(No_3)_2$ added. In this case the total algal growth reached a density of 2590 cells per mm³. This increase in growth is an indication that nitrate was the factor limiting population growth in the original sample. When nitrate was present in sufficient amounts and another nutrient was the limiting factor, the nitrate-added culture did not differ significantly from the control in the size of the algal population supported.

RESULTS

The *K*-values obtained during the present study were plotted to illustrate seasonal fluctuations in the nutrient content of the pond water and to compare results obtained upon the addition of nutrients.

Lower Pond

Control samples (Fig. 2) show seasonal variations in the ability of the water to support plant growth. Samples collected during November and December supported the greatest amount of *K. subsolitaria.* There was a rapid decline in the nutrient content of the water during January, as

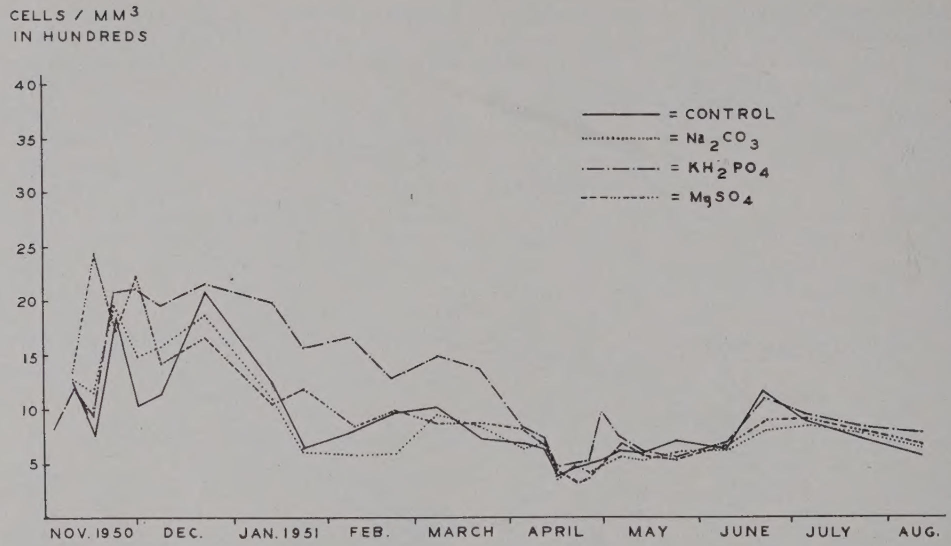

FIG. 2. *K*-values obtained from samples of water from Lower Pond. Shown are the control and samples to which was added carbonate, phosphate, or sulfate.

reflected by the relatively small populations in the index alga supported at this time. This was followed by a slight increase in nutrients during February and March. The nutrient content of the water then declined during late March and April and reached the lowest levels recorded. During this period there was a noticeable increase in algal production, an algal mat being produced at the shallow end of the pond, and the water becoming more turbid. The ability of control samples to support growth of the index alga increased slowly until another peak was reached in June. This was followed by a steady decline during July and August.

The addition of carbonate and sulfate (Fig. 2) did not produce results significantly different from those of the control. This would indicate that these nutrients were not limiting factors for growth of the index alga in water from Lower Pond. Because *K. subsolitaria* is an alga of quite generalized nutritional requirements, the implication is that carbonate and sulfate were not major factors limiting phytoplankton growth in this pond during the present study. Also, since carbonate was added in the form of Na_2Co_3, and sulfate as $MgSO_4$, sodium and magnesium cations were present in the pond water in quantities sufficiently above the level where they might be important factors limiting phytoplankton production.

Samples to which phosphate was added yielded somewhat different results (Fig. 2). During the winter months, samples with phosphate added supported notably larger populations of *K. subsolitaria* than the controls. During April, at the time of the phytoplankton pulse in the pond, there was a great decrease in the ability of samples to support growth. At this time, and continuing throughout the summer, there was no significant difference in size of populations supported by the phosphate-added samples and those of the controls. These results indicate that available phosphate was an important limiting factor during the winter months, but became less important during the spring and summer.

Since phosphate was added in the form of KH_2PO_4, it was necessary to determine whether potassium, rather than phosphate, was the substance stimulating increased algal growth. A solution of NaH_2PO_4 was made up, containing the same concentration of phosphate as did the KH_2PO_4. For several weeks, whenever samples were taken, duplicate culture samples were established, using each of the two phosphate solutions in equal amounts. There was no significant size difference between the algal populations supported by the soduim and potassium phosphate cultures. It was concluded, therefore, that phosphate was the ingredient producing increased algal growth in the phosphate-added samples.

The samples to which a standard amount of nitrate was added (Fig. 3) yielded the reverse of what was obtained by the phosphate-added cultures. Throughout the winter the samples with nitrate added did not support significantly larger

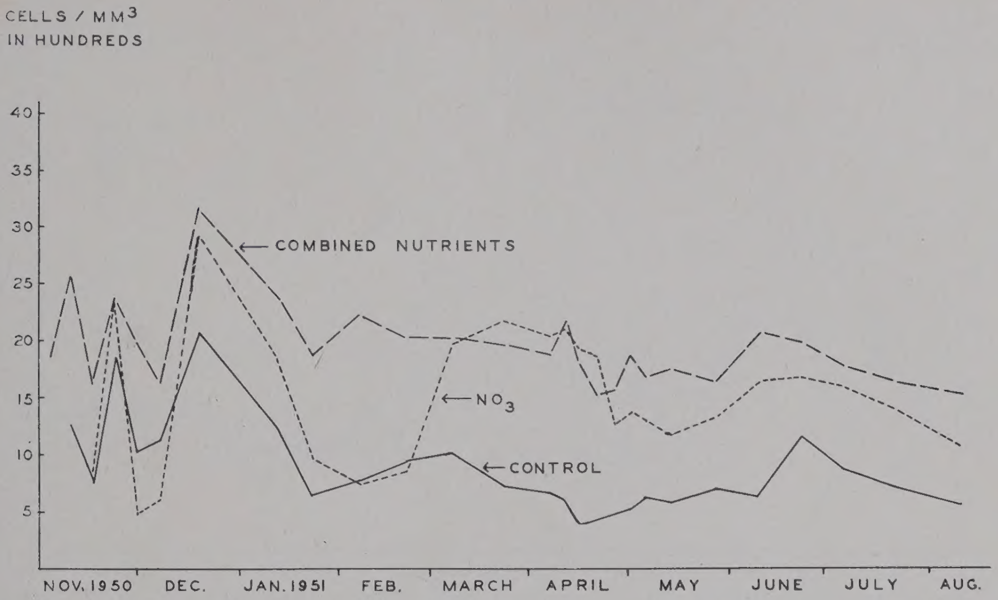

FIG. 3. Results obtained upon addition of nitrate and of the combined nutrients to samples for Lower Pond. Control results are included for comparison.

populations of the assay organism than did the control samples. Beginning in late February and continuing throughout the spring and summer, the nitrate-added cultures supported much larger populations of the index alga than did the corresponding control samples. Nitrate suddenly became the dominant limiting factor during the period of the spring phytoplankton bloom. At this time, the nitrate-added cultures yielded their greatest increase in growth over corresponding control cultures. During April, and through the summer, the nitrate-added cultures continued to support significantly larger populations of *K. subsolitaria* than did the controls, although the differences were not as great as during March and early April.

This indicates that during the spring nitrate replaced phosphate as a limiting factor for plant growth. This nitrate deficiency appeared rather suddenly and assumed its greatest proportion at the time of rapidly increasing phytoplankton production in the pond. During the remainder of the study nitrate remained the most important limiting factor, although its addition to samples taken during the summer did not produce the large populations of *K. subsolitaria* supported during the spring.

The addition of standard amounts of all four nutrients produced consistently greater amounts of algae (Fig. 3). The greater densities evidently are the product of the added nutrients rather than the original nutrient content of the water sample. The apparent explanation is that the addition of the 3 gamma of phosphate in the "all-four" sample at a time when phosphate was the limiting factor evidently was more than sufficient to permit the utilization of all the natural nitrate. The additional nitrate made available the remaining excess of phosphate, resulting in greater populations than those supported by the phosphate-added samples. When nitrate was the limiting factor, the opposite would be true.

Upper Pond

A similar study of Upper Pond was made, water samples being removed on the same dates and treated in the same manner as were samples from Lower Pond. Results (Fig. 4) were, in general, qualitatively similar to those of Lower Pond. There was an accumulation of nutrients during December, followed by a nutrient decrease during January. In February, March, and early April, the nutrient content of the water reached its greatest concentration, as indicated by the very high *K*-values obtained from the control samples. Samples taken during April supported smaller populations of the index alga, indicating that the productive capacity of the water was not as great. Since this occurred during the period of greatest phytoplankton production, it is assumed that the accumulation of nutrients was diminished by the photosynthetic activity of aquatic plants. There

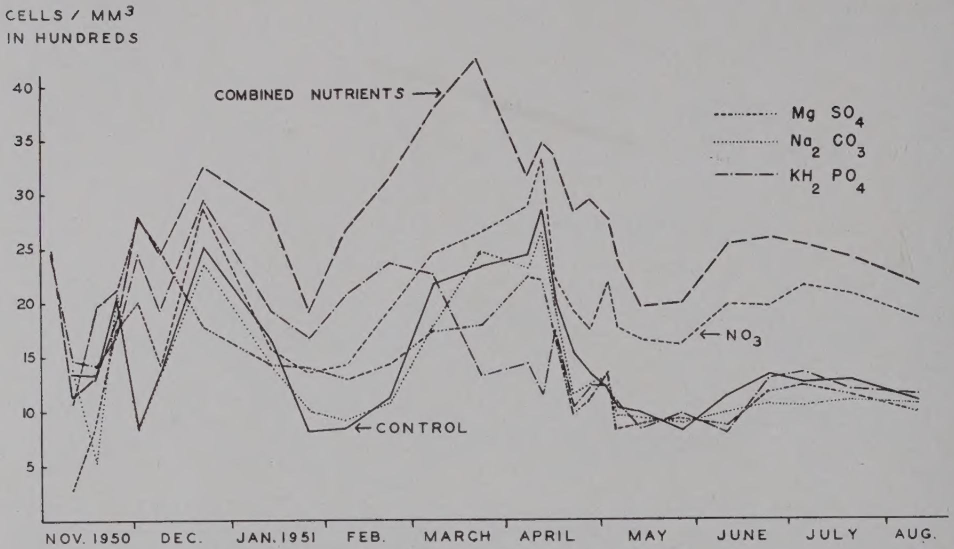

FIG. 4. Results from samples of water from Upper Pond. Shown are the control and samples to which were added carbonate, nitrate, phosphate, sulfate, or the combined nutrients.

appears to have been a slight built-up of nutrients during June, followed by a decrease in July and August. This was also true of Lower Pond.

The samples from Upper Pond (Fig. 4) to which standard amounts of inorganic nutrients were added exhibited results similar to those of corresponding samples from Lower Pond. Again, cultures with Na_2CO_3 or with $MgSO_4$ added did not support larger laboratory populations of the index alga than did the corresponding control samples, indicating that these nutrients were not limiting factors in Upper Pond during the course of this study.

Samples to which nitrate or phosphate was added displayed trends very similar to results obtained from Lower Pond. Phosphate appeared to be a limiting factor during the winter, but decreased in importance during spring and summer. In fact, during March, phosphate-added samples supported much smaller populations than did the corresponding control samples. It is possible that this phenomenon was brought about by creating an excess of phosphate in these samples, but the actual cause is obscure.

The seasonal distribution of nitrate demand in Upper Pond (Fig. 4) also resembled that of Lower Pond, nitrate appearing as a limiting factor during April, and continuing so throughout the remainder of the study. The combined nutrient samples again supported consistently larger populations of *K. subsolitaria* than did any of the other samples.

From November through most of February, there appear to be no significant differences between the amount of algal growth supported by the control samples from Upper and Lower Ponds (Fig. 5). During March and April, however, there is a very striking difference in *K*-values obtained from corresponding control samples from the two ponds. In Upper Pond, the nutrient content of the water increased very decidedly, reaching a peak in early April. This was followed by a relatively sudden decrease in available nutrients in the water, as indicated by the decrease in density of *K. subsolitaria* populations supported by these samples. Corresponding control samples from Lower Pond indicate only a relatively slight increase in available nutrients during this period. This obvious difference in ability of control samples to support populations of the index alga continued throughout the summer, although the difference was not as great as during the period of maximum phytoplankton production.

A comparison of the samples to which the combined nutrients were added (Fig. 5) indicates similar trends, the greatest difference in nutrient content of the water being observed at the time of the spring phytoplankton bloom. This ability of Upper Pond waters to support larger populations of the index alga than Lower Pond samples became noticeable in the combined nutrient sam-

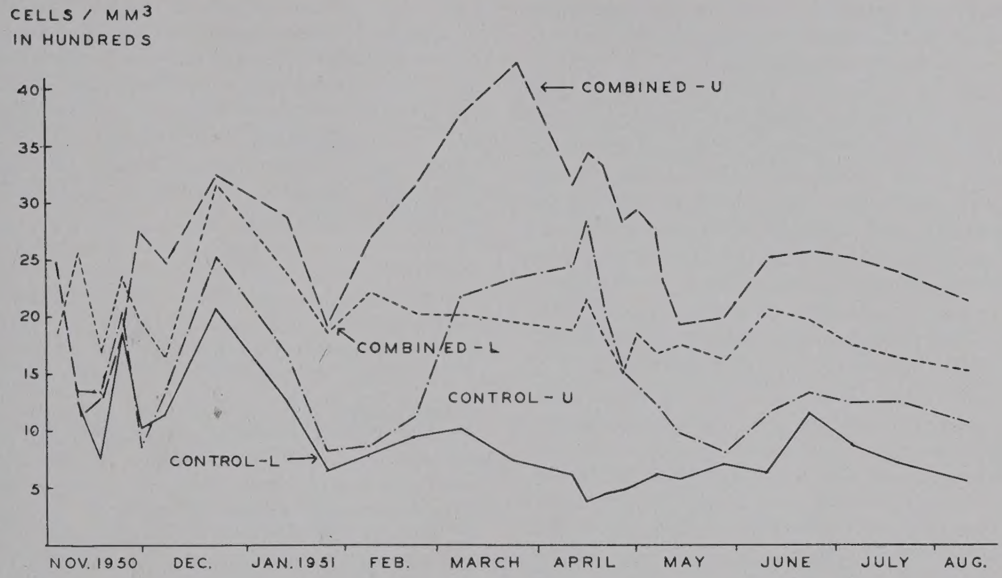

FIG. 5. A comparison of the two ponds. Plotted are the results obtained from control samples as well as those to which were added standard amounts of all four nutrients.

ples almost three weeks earlier than in the control samples.

These results are probably attributable to the fact that Lower Pond was quite productive, supporting a relatively large phytoplankton and aquatic plant population. Nutrients were probably being utilized as rapidly as they became available. In Upper Pond, however, little plant growth was present, allowing for an accumulation of nutrients. Thus, there seems to be an inverse correlation between potential productivity and actual plant production.

DISCUSSION

The application of the biological test to the study of two farm ponds yielded significant qualitative and quantitative results. Nitrate and phosphate were, at times, present in limiting amounts. Carbonate, sulfate, magnesium, calcium, sodium, and potassium were present in excess in all samples tested. This further supports the generalization that in small lakes or ponds all nutrients are probably present in excess except nitrate and phosphate (Hutchinson 1944).

Phosphate limited phytoplankton growth during the winter. Nitrate became limiting during the spring and summer. The fields surrounding Upper Pond were fertilized with 250 pounds of standard 5-10-5 (NH_4-P_2O_5-K_2O) fertilizer during the third week in April, 1951. This was after nitrate had replaced phosphate as the factor limiting phytoplankton growth in both ponds, and nitrate remained the factor limiting growth during this period. The gradual loss of fertilizer from the watershed by leaching or runoff may have produced the slight increase of growth obtained during June and July, but this can only be surmised.

Throughout the study, samples from Upper Pond consistently supported larger populations of *K. subsolitaria* than corresponding samples from Lower Pond. This was true for the controls as well as for all cultures to which nutrients were added. Correlated with this, Lower Pond contained more aquatic growth than did Upper Pond. Although no quantitative study was made of phytoplankton or other aquatic plants, Lower Pond was obviously more productive. Cattails and other higher aquatics grew abundantly at the shallow end of the pond, and an algal mat was present over a part of the pond during the summer months. Upper Pond, being newly constructed at the time of this study, contained no higher plants nor shore growth, and a sparse phytoplankton population. This leads to the conclusion that there is an inverse relationship between potential productivity and actual plant production. The small amount of growth in Upper Pond permitted nutrients to accumulate. In Lower Pond, the comparatively large amount of phytoplankton and aquatic plant growth evidently assimilated the limiting nutrients almost as rapidly as they became available. The quantitative data presented regarding the nutrients available for potential plant growth would have been more meaningful, therefore, if correlated with quantitative information on actual plant production.

While the available nutrients set a basic limit to phytoplankton production, other factors actively influence growth and reproduction. During the winter months, temperature and sunlight assume greatest importance as factors limiting phytoplankton growth. Turbidity, by influencing light penetration, acts at times to affect phytoplankton abundance (Chandler 1942a, 1942b, 1944; Chandler and Weeks 1945). Upper Pond was quite turbid during the first year following construction. This factor may have limited productivity in Upper Pond during the present study, since the available nutrients could have supported populations larger than those observed.

This biological test quantitatively measured nutrient deficiencies by comparing the population supported by a control sample with growth in test samples to which specific nutrients were added. Assuming that each algal cell assimilates an equal amount of the nutrient, then the quantity utilized per cell is of the magnitude of one micro-gamma. Colorimetric or spectrophotometric methods are sensitive to about one gamma per liter of water. Hence, the proposed method appears to be potentially more sensitive.

Biological tests are extremely sensitive and measure only the nutrient actually available to the algae. Chemical tests, whether measuring a specific nutrient or component of a nutrient, cannot give us this information. The application of the suggested objective method for determining population density should yield quantitative results at a cellular level of utilization for any nutrient analyzed.

The proposed method may provide a suitable tool for studying the artificial fertilization of farm ponds. While many workers have had success in increasing fish growth by the addition of inorganic nutrients to ponds (*e.g.* Smith and Swingle 1939, Surber 1948, Ball 1949, Swingle and Smith 1950), little is known about the many intermediate steps involved between the addition of nutrients and the increased fish production. Edmondson and Edmondson (1947) point out that while it is possible to obtain satisfying yields of fish by fertilizing without studying intermediate steps, a scientific investigation of food chains and nutrient cycles is concerned with more than the end point in the chain. The basic approach should center about the problem of the utilization of the added inorganic nutrients by the phytoplankton. These nutrients must first be assimilated by the primary producers, which form the fundamental source of energy for the food chain. Assay of nutrients with *K. subsolitaria,* when correlated with phytoplankton production and chemical analysis of the water, suggests a quantitative method for evaluating the immediate effect of fertilizer on the trophic-dynamic balance of a lake or pond and, therefore, its ultimate effect in increasing fish production.

SUMMARY

1. A method is presented for determining quantitatively the nutrients available for plant growth in natural waters, using a pure culture of the green alga *Kirchneriella subsolitaria* G. S. West as an indicator organism.

2. The method was applied to a study of two farm ponds. From Nov. 3, 1950, to Aug. 10, 1951, water samples were brought to the laboratory and filtered to remove all plankton.

3. Six 500-ml samples from each pond were inoculated with *K. subsolitaria.* One sample from each pond was designated as a control. Others had added either Na_2CO_3, $Ca(NO_3)_2$, KH_2PO_4, $MgSO_4$, or all four nutrients.

4. Temperature and light were controlled. Daily cell counts were made, using Sedgwick-Rafter counting chambers.

5. The statistical application of the logistic function and minimum Chi-square were employed as an accurate and objective method for determining population density.

6. Both ponds varied seasonally in ability to support algal growth. As indicated by the control cultures, nutrient content reached a peak in November and December, declined sharply in January, increased during February and early March, and again declined during late March and April.

7. The addition of Na_2CO_3 and $MgSO_4$ to samples did not increase the ability of the water to support growth.

8. In both ponds, phosphate appeared as the major limiting factor during the winter. In March, nitrate replaced phosphate as the limiting nutrient, continuing so through the summer.

9. Samples from Upper Pond were potentially more productive than corresponding samples from Lower Pond. Lower Pond was actually more productive. There appears, therefore, to be an inverse correlation between potential and actual productivity.

10. It is suggested that the proposed method may present a useful approach to the pond fertilization problem.

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ECOLOGY OF CHAOBORUS (DIPTERA: CULICIDAE) IN AN ONTARIO LAKE

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INTRODUCTION

Much of our knowledge of Chaoborus in North America lakes is based on studies by Juday (1921) and Eggleton (1931). These authors followed the numbers of larvae in the profundal zone over periods of a year or more. They reported tremendous variations in number between midsummer and midwinter. Eggleton (1931) estimated that the concentration of Chaoborus at depths of 18 to 18.5 meters in Third Sister Lake, Michigan varied from 1500 to 71,500 individuals per square meter of lake bottom during the year.

A similar variation was discovered in the number of Chaoborus larvae in the deepest part of Little McCauley Lake, Algonquin Park, Ontario. Observations were made on both benthic and limnetic habitats and included all but the shallowest parts of the lake. Estimates were derived for the total number of larvae or pupae in each of several zones of the lake over an 18-month period. From these data it was possible to demonstrate that the great annual variation in number of

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Chaoborus in the profundal zone primarily results from semi-annual migrations of the larvae.

It is a pleasure to acknowledge my indebtedness to Profs. F. E. J. Fry, R. R. Langford, and F. P. Ide for assistance during the investigation and for criticism of the manuscript. Prof. Langford also supplied data on the chemical and physical conditions of the lake. The study was part of a cooperative project by the Research Division of the Department of Lands and Forests, Province of Ontario, and by the Ontario Fisheries Research Laboratory, Department of Zoology, University of Toronto. This paper is extracted from a thesis presented at the University of Toronto, November, 1949.

THE LAKE

Little McCauley Lake is located in the Canadian Shield of Canada in Algonquin Provincial Park about 150 miles north of Lake Ontario. It has an area of 49.6 acres and a mean depth of 4.2 meters. The area of contour intervals is as follows: 0-3 meters, 12.0 acres; 3-6 meters, 30.6 acres; 6-8 meters, 3.9 acres; 8-10 meters, 3.1 acres. The basin is long and narrow and is divided into two depressions each of 10 meters maximum depth. The bottom within the 3-meter contour is of soft, black ooze. The color of the water is 25 mg/liter on the platinum scale, and the turbidity is equivalent to 2.0 ppm of silica. The Secchi disc disappears at 4.5 meters and the depth of one percent light penetration is 5.5 meters.

During the summer of 1947 5 tons of commercial fertilizer were added to the lake (Langford 1950). An additional 4 tons were added during 1948. The lake suffered from severe oxygen depletion below the thermocline during midsummer. This effect was more pronounced after the above chemical treatment.

METHODS

Bottom samples were taken at scattered points over the area of the lake with a 9-inch Ekman dredge (a 6-inch dredge was used during April and May, 1948). The samples were washed through a pair of 30- and 50-mesh screens and the organisms were preserved in 10 percent formalin. During the study 341 bottom samples were taken on 12 trips from June, 1947 to November, 1948. The free-water habitat was sampled by means of 146 total vertical-net hauls with a 12.6-inch-diameter tow net of 50-mesh nylon marquisette on 8 occasions during the summer of 1948.

Population estimates based on these samples have inherently great possible errors, as any reader familiar with such field studies is well aware. Therefore a rigorous statistical treatment of these few samples from a 50-acre lake seems unwarranted.

NOCTURNAL MOVEMENTS OF CHAOBORUS

A series of 25 total vertical-net hauls was taken at hourly intervals from the west depression of Little McCauley Lake on July 3-4, 1948. The results are given in Figure 1 as the number of individuals per column of water one square meter in area and 10 meters deep (from the botton of the lake to the surface). Three kinds of individuals were recognized: recently hatched larvae, overwintered larvae, and pupae.

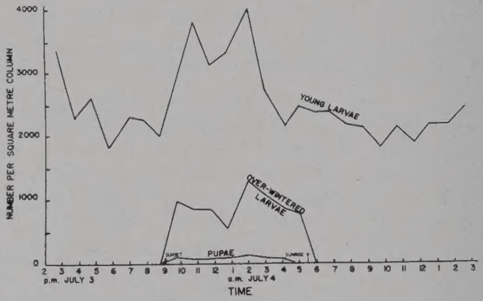

FIG. 1. The number of Chaoborus larvae and pupae per square meter column (0-10 meters) captured in total vertical net hauls from the west depression of Little McCauley Lake, July 3-4, 1948.

Evidently young larvae were present in the water at all times. Between sunrise and sunset additional young larvae, overwintered larvae, and pupae were collected. This behaviour of the older larvae and pupae is similar to that described by Juday (1921). Berg (1937) explained, on the basis of studies in aquaria, that the newly hatched larvae are positively phototactic while slightly older larvae, and pupae are negatively phototactic. However Wesenberg-Lund (1943) wonders how creatures buried in the sediment could detect the difference between day and night at the water surface.

The proportion of larvae which migrate each night is shown in Table I. Dredge and net samples were taken from the west depression of Little McCauley Lake on 7 occasions during May-November, 1948. The number of larvae or pupae in the water column over the 10-meter depth was estimated for day and night. These values were subtracted from each other to obtain the nocturnal increase. This latter value is expressed as a percentage of the daytime benthic population at 10 meters.

TABLE I. Number of larvae per square meter in the benthic habitat during the day and in the limnetic habitat during day and night in the west depression of Little McCauley Lake (depth 10 meters), May-November, 1948

Date 1948	LARVAE OR PUPAE PER SQUARE METER				
	Day benthic	Day limnetic	Night limnetic	Nocturnal increase	Percentage migration
May 7†.....	16,900*	0	1,916	1,916	11
June 1......	11,535	0	2,545	2,545	22
23.....	4,970	491	1,688	1,197	24
July 3	3,249*	2,275	4,030	1,755	54
August 15...	7,600	2,080	3,328	1,248	16
16...	7,600	2,912	4,750	1,846	24
November 4.	22,260	26	917	891	4

*Value interpolated.
†East depression.

The strongest migrations occurred during June-August when from 16 to 54 percent of the benthic larvae were represented in the free-water habitat at night. During May 11 percent participated in the movement, and in November, 4 percent. Evidently the larvae were most active during the summer months. In Little McCauley Lake an average of 22 percent of the benthic population became limnetic at night. Juday (1921) estimated that from one-third to one-half of the older larvae in Lake Mendota, Wisconsin became limnetic at night. Other authors report various results. In some lakes older larvae are taken free-swimming during the day (Juday 1921; Eggleton 1932; Berg 1937).

Although some aspects of the responses of the larvae remain obscure they do provide a mechanism by which migration across the lake bottom could occur. Obviously it is not necessary to assume that the larvae return to the same place on the bottom which they left the night before. It is thus that Borutsky explains the semi-annual migrations of Chaoborus larvae and pupae in White Lake, Russia: a shoreward, adlittoral migration during the spring and early summer, and an ablittoral migration in the fall and early winter.

LIFE CYCLE

Exclusive of the 0-to-3-meter zone which was found to contain relatively few larvae (average population 12.4 million), variations in the number of larvae in the lake are shown in Figure 2. The results are expressed in total abundance (concentration x area of zone) rather than in abundance per unit area because it is desired to demonstrate shifts of population between zones of unequal extent.

The total population of Chaoborus (uppermost curve of Fig. 2) passes from a low point in mid-June to a high in September and then decreases

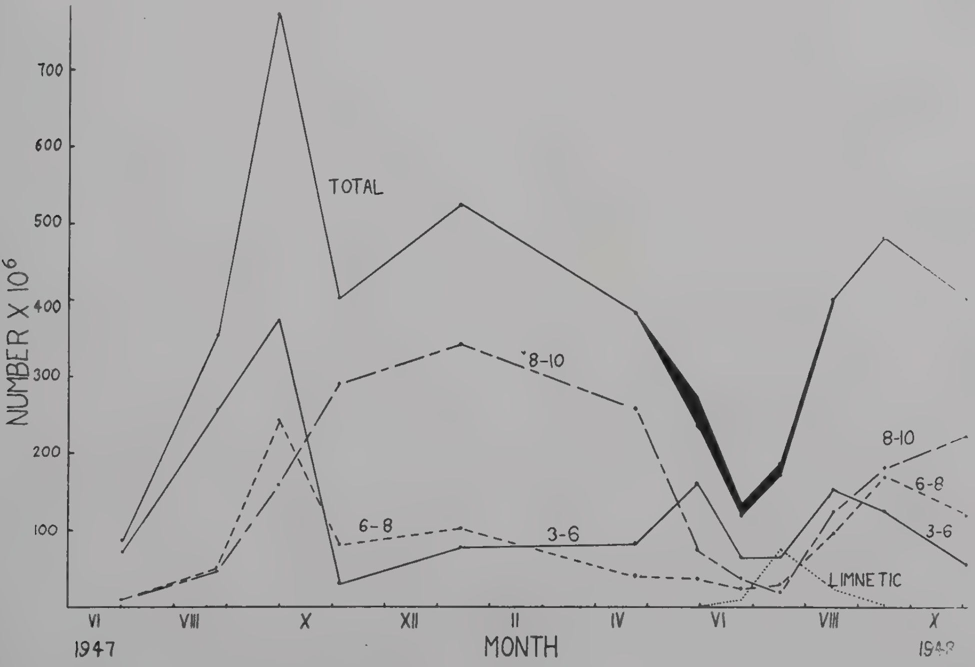

FIG. 2. The number of Chaoborus larvae and pupae (pupae indicated by black shading) in several zones of Little McCauley Lake from June, 1947 to November, 1948.

throughout the remainder of the cycle. The time of reproduction is evidenced by the appearance of pupae between the months of May and August, 1948 (shown by black shading on the total curve), and by the presence of young, daytime-limnetic larvae between the months of June and September (dotted curve in Fig. 2). The peak number of pupae, 35.6 million, occurred on May 29, and the peak number of young larvae, 76 million, on July 17. Judging from the times of these maxima the largest emergence of adults, with subsequent mating and egg-laying, must have occurred during June. Miller (1941) recorded emergence of Chaborus from nearby Costello Lake in Algonquin Park during June, July, and the first half of September.

The larval period is evidently of one year's duration in Little McCauley Lake. Generations overlap during midsummer,[2] hence during 1948 the minimum population (133 million on June 23) did not fall below about one quarter of the maximum (482 million on September 16).

It was shown in Figure 1 that young larvae were found free-swimming both day and night. Juday (1921) estimated that the larvae descend from the limnetic to the benthic habitat during the first week or 10 days of development. On this basis the average daytime-limnetic population of 1948 should be represented many fold in the benthic population of September. There must be a constant turnover of the limnetic population—eggs hatch, the larvae spend at least a week continually in the free-water habitat, and then live in the benthic habitat during the day.

The 1948 limnetic population in millions of larvae was as follows: June 1, 0.0; June 23, 9.7; July 3, 45; July 15, 76; August 15, 24.3; September 15, 4.6. A single net haul, taken at 8:40 a.m. on November 5 and yielding two larvae, is disregarded. This amounts to an average of 23 million daytime-limnetic larvae in the lake during 11 weeks from June until mid-September. Assuming that these larvae were completely replaced each week, a total benthic population of 253 million would be predicted for September. The estimate from dredging was 478 million (Fig. 2).

The difference between these two estimates may be due to larvae entering the bottom before the age of one week, or to other errors in the data. However the calculations illustrate some of the problems involved in working out this life cycle, and call attention to the peculiar behaviour of the young larvae.

Semi-annual Migrations

Population changes in three benthic zones of the lake (3-6, 6-8, and 8-10 meters) are shown in the lower curves of Figure 2. Evidently numbers increased in all zones between June and September, 1947. However during October there was a very sharp depopulation of the two shallower zones, while the number of larvae at 8-10 meters continued to increase. Likewise during autumn, 1948 the population at 3-6 meters decreased after the middle of August, and that at 6-8 meters fell off after the middle of September, while numbers at 8-10 meters continued to increase from the middle of July.

From the previous discussion it is evident that the larval population is largely renewed between June and September. Therefore the continued increase at 8-10 meters after September must be ascribed to migrations from the shallower zones. This is the ablittoral migration of Borutsky. It continued at least until January, 1948, when 343 million larvae, 65 percent of the population, had squeezed themselves into the 3.1 acres of sediment below the 8-meter depth contour.

The shoreward migration is seen first in an apparent lack of mortality in the shallowest zone. Between January and April, 1948, the 8-to-10-meter zone lost 83 million, and the 6-to-8-meter zone lost 63 million larvae. However the 3-to-6-meter zone gained 2.4 million larvae over this time.

A shoreward migration is clearly evident in the data of April 23-May 29, 1948. During this time there was a loss of 185 million at 8-10 meters, a loss of 4 million at 6-8 meters, and a gain of 77 million at 3-6 meters. The latter gain included 30 million pupae, or 22.8 percent of the population at that depth. This abundance of pupae is indicative of a considerable drain upon the larval population through transformation, which could only be offset through continued migrations from deeper areas of the lake.

This shoreward movement probably continued during June and July for the population at 3-6 meters remained at 51 to 55 million. Numbers at 6-8 meters reached a low of 23 million on June 23, and the minimum at 8-10 meters was 15.8 million on July 17.

Most of the pupation evidently occurred in the shallower depths. During 1948, 78 percent of the pupae collected occurred at 3-6 meters, 10 percent at 6-8 meters, and 12 percent at 8-10 meters. Scott and Opdyke (1941) and Lindquist and Deonier (1942) reported inshore migrations of larvae or pupae of Chaoborus before the time of emergence. Borutsky (1939) suggested that the larvae migrate to shallower depths where the higher temperature of the water favors transformation.

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[2] Overlapping of generations may be accounted for by the fact that two species, *Chaoborus punctipennis* Say and the larger *C. flavicans* Meigen (=C. *albipes* Johannsen), were identified in the collections by E. S. Deevey.

ADDENDUM

Additional samples were taken during 1949 and 1953 to follow the effect of the chemical treatment of the lake. The following estimates of Chaoborus population were obtained (millions of larvae or pupae in the lake bottom in the 3-to-10-meter zone): 1949 (81 samples); April 28, 222; July 7, 148; August 20, 237. 1953 (77 samples); July 23, 23; August 24, 41.

Numbers during April and August, 1949 were smaller than corresponding values of 1948, the July population was somewhat higher. In 1953 the July population was one-third, and the August population one-ninth of its size in former years.

This great decrease in the number of Chaoborus in the lake may be related to eutrophication by the addition of chemical fertilizer. Evaluation of this treatment must await a series of reports now being prepared by the Ontario Department of Lands and Forests.

SUMMARY

1. The nocturnal movement of Chaoborus larvae and pupae was demonstrated in an Ontario lake. They rise up from the bottom ooze into the free-water layers at sunset and return at sunrise. An average of 22 percent of the benthic larvae participated.

2. Recently hatched larvae spend the first few days of their existence continually in the free-water habitat, and subsequently dwell in the bottom ooze during the day.

3. The life cycle of Chaoborus in Little McCauley Lake is of one year's duration.

4. During the fall and early winter the abundance of bottom-living larvae decreases in the shallow areas (3-8 meters) and greatly increases in the deep (8-10 meters)—an ablittoral migration.

5. During the spring the abundance of larvae decreases in the deep and increases in the shallow areas—an adlittoral migration.

6. The tremendous annual variation in the concentration of larvae in the profundal zone was correlated with the semi-annual migrations of the larvae and pupae.

7. During 1948 the total population of Chaoborus within the 3-meter contour of Little McCauley Lake varied from 108 million in June to 488 million in September—values interpreted as the minimum and maximum populations of that year.

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A STATISTICAL EVALUATION OF STREAM BOTTOM SAMPLING DATA OBTAINED FROM THREE STANDARD SAMPLERS

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Investigation of invertebrate macro-bottom fauna in stream sanitation, fisheries biology, and limnological stuides has led to a certain degree of standardization of techniques and equipment for stream bottom sampling. Research of this kind, however, still in its youth, demands much further improvement and refinement of presently accepted equipment and techniques in order to surmount the many special problems inherent in stream survey work. A knowledge of the number of samples needed to give an adequate faunal picture at any part of a stream would be highly desirable.

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One of the goals of the Biology Section of the Sanitary Engineering Center at Cincinnati, Ohio, in its stream pollution surveys has been the improvement of methods and equipment. The lack of a statistical criterion for evaluating the efficiency of different sampling devices currently in use is an obstacle to further progress.

The present paper introduces such a criterion and applies it to data derived from a special series of samples taken in a small midwestern stream. This stream, Lytle Creek, located about forty-five miles northeast of Cincinnati, has been the subject of extensive research by the Public Health Service (U. S. Department of Health, Education, and Welfare) into the dynamics of stream pollution. Lytle Creek is ideal for such study since the bulk of its pollution is received from one source, a sewage treatment plant from which effluent enters the stream about seven miles above its mouth. Lytle Creek is a permanent stream, approximately 11 miles long and 3 to 35 feet wide during low water stages. The principal sources of flow are drainage from adjacent agricultural areas, and the effluent from the Wilmington Sewage Treatment Plant. During periods of low flow and high temperatures the stream exhibits all degrees of pollution including septic, recovery, and clear water zones (Gaufin and Tarzwell 1952).

Two sections of the creek were sampled during the course of the present study, namely, the lower end of the recovery and the mid portion of the clean water zone. A total of sixty samples was collected: ten each from a marginal, pool, and riffle area at each station. These areas are designated respectively, by station, as 1a, b, c, and 2a, b, c. The marginal samples were taken with a special long handled dip-strainer, the pool samples with an Ekman dredge, and the riffle samples with a Surber square foot sampler. Each of these devices is presently believed to be the most suitable in its area. The samples were preserved in quart jars of 10% formaldehyde solution for later study. In the laboratory, the fauna was separated from the debris and identified to genus and species wherever possible.

Bottom types were not differentiated, and little effort was made to select sampling plots on the basis of potential fruitfulness. Hence the sampling efficiencies calculated here represent minimum values which in routine practice might well be improved upon by careful selection of areas, bottom types, and comparable depths and currents.

STATISTICAL METHOD AND RESULTS

Given a series of n samples (in this study, ten at each station) and an observed number of different species, it is desirable to estimate the proportion of these species which would have been detected, on the average, by a smaller number of samples, say $k < n$.

This may be done by drawing all possible sets of k samples from the n study samples and averaging the number of different species observed in each of these sets. The number of sets so obtained is given by the familiar combinatorial symbol

$$C^k_n = \frac{n!}{k! \quad (n-k)!}$$

Admittedly the various sets are highly correlated (except for $k = 1$) since they share the same study samples. However, the mean obtained is not a biased estimate, and its expected value (*i.e.,* the mean value over all possible sets of k samples which could be obtained from the stream) is the same as that of a mean based on completely independent sets.

Since one of the purposes of this study was to investigate sampling efficiency, the number of study samples taken was considerably larger than might be the case in routine sampling. When n is large the labor of counting the number of different species present in each set of k samples becomes excessive. It is then worthwhile to develop a formula for determining the mean number of species observed.

Reference is made in the following to new species yielded by the "k-th sample drawn." This does not refer to the k-th sample of the particular set of n samples studied here (whose order need not concern us), but rather to a general k-th sample of which any sample in the present series might well be a model.

Let P_k represent the average[3] probability that a species will be found in the k-th of a set of $k \leqq n$ samples but in no previous sample, given that it has appeared in at least one of the present set of n samples. Then, $P_k =$ (Probability of a species having been found in exactly one sample out of n) $\times$ (Probability being found in k-th sample but in none previous, given found in one sample out of n) $+$ (Probability of a species having been found in exactly two samples out of n) $\times$ (Probability being found in k-th sample but in none previous, given found in two samples out of n) + ... + (Probability of a species having been found in $n - k + 1$ samples out of n) × (Probability being found in k-th sample but in none previous, given found in $n - k + 1$ samples out of n).

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[3] Since species vary in their abundance, P_k will not be constant for all species. Hence, P_k itself is not of much intrinsic value but is merely a means to an end.

The n observed samples provide a distribution of species according to the number of samples in which each species has appeared. Obviously, the value of n limits the range of k for which information can be obtained.

When $k = 1$,

$$P_1 = \sum_{i=1}^{n} [(i/n)/(S_i/S)],$$

where S_i is the number of different species appearing in i out of n samples, and S is the total number of species observed.

When $k = 2$,

$$P_2 = \sum_{i=1}^{n-1} [(n-i)/n]\ [i/n-1]\ S_i/S$$

In general,

$$P_k = \sum_{i=1}^{n-k+1} \frac{C^i_{n-k+1} \times (i)}{C^i_n \times (n-k+1)} S_i/S \quad (1)$$

It is not difficult to show that $\sum_{k=1}^{n} P_k$ (as given by Eq. 1) = 1, a necessary condition for a complete discription of the n observed samples. Then SP_k is the average number of *new* species contributed by the k-th of a set of samples drawn from n, and $S \sum_{k=1}^{k'} P_k$ is the average number of different species observed in sets of k' samples drawn from n.

The computation of P_k is basically a matter of computing the coefficients $\frac{C^i_{n-k+1}\ (i)}{C^i_n\ (n-k+1)}$, which may be denoted by $a_{i,k}$. The formula $a_{i,k+1} = [(n-k-i+1)/(n-k)]a_{i,k}$ is helpful in writing the coefficients for successive values of k once those for $k = 1$ are obtained. As noted above, these latter are merely i/n $(i = 1, 2, \ldots, n)$.

The coefficients for $n = 10$ are listed in Table I. Note that the numbers are kept in integral form by tabling not $a_{i,k}$ itself, but rather $a_{i,k}$ times a constant (given at the head of each column) which varies with k. This constant is $k\,C^k_n = (n!)/(k-1)!\,(n-k)!$. The rows of the table are symmetrical so that once the values up to $k = n/2$ (for n even) or $k = (n+1)/2$ (for n odd) are obtained, the remaining values may be written without further calculation.

The observations made at Station 1a will be used to illustrate the calculation of P_k. Reference is made to Table II, Column 1a, where the fifty species observed at this station are distributed according to the number of samples in which each species appeared. Similar distributions are shown in Table II for each of the other sampling points.

For example, at Station 1a, nineteen species were found in just one sample—not all in the same one, of course; seven other species were found in

TABLE I

Coefficients $a_{i,k} = \frac{C^i_{n-k+1}\quad (i)}{C^i_n\quad (n-k+1)}$ (see Equation 1), for $n = 10$

k	1	2	3	4	5	6	7	8	9	10
i	$(10a_{i,1})$	$(90a_{i,2})$	$(360a_{i,3})$	$(840a_{i,4})$	$(1{,}260a_{i,5})$	$(1{,}260a_{i,6})$	$(840a_{i,7})$	$(360a_{i,8})$	$(90a_{i,9})$	$(10a_{i,10})$
1....	1	9	36	84	126	126	84	36	9	1
2....	2	16	56	112	140	112	56	16	2	
3....	3	21	63	105	105	63	21	3		
4....	4	24	60	80	60	24	4			
5....	5	25	50	50	25	5				
6....	6	24	36	24	6					
7....	7	21	21	7						
8....	8	16	8							
9....	9	9								
10....	10									

exactly two samples, the particular pair varying from one species to another; six other species were found in exactly three samples, and so on.

Using the coefficients given in the first column ($k = 1$) of Table I, P_1 at Station 1a is given by the sum:

$$P_1 = \sum_{i=1}^{10} a_{i,1}\,(S_i/S) = (1/50) \sum_{i=1}^{10} a_{i,1}\,S_i$$

$$= (1/50 \times 10)\ [1 \times 19 + 2 \times 7 + 3 \times 6 + 4 \times 5 + \ldots + 10 \times 5]$$

$$= .3560,$$

and

$$P_2 = \sum_{i=1}^{9} a_{i,2}\,(S_i/S)$$

$$= (1/50 \times 90)\ [9 \times 19 + 16 \times 7 + 21 \times 6 + \ldots + 9 \times 2]$$

$$= .1498,$$

while, for example,

$$P_5 = \sum_{i=1}^{6} a_{i,5}\,(S_i/S)$$

$$= \frac{1}{50 \times 1{,}260}\ [126 \times 19 + 140 \times 7 + 105 \times 6 + \ldots + 6 \times 1]$$

$$= .0692,$$

and

$$P_8 = \sum_{i=1}^{3} a_{i,8}\,(S_i/S)$$

$$= \frac{1}{50 \times 360}\ [36 \times 19 + 16 \times 7 + 3 \times 6]$$

$$= .0452$$

These and all other computed values of Pk are listed in Table III.

TABLE II. Distribution of Species According to the Number of Samples in which each Species Appears, by Station

No. of Samples	1a	1b	1c	2a	2b	2c
1.......	19	26	11	24	19	17
2.......	7	5	5	9	11	10
3.......	6	8	4	5	10	3
4.......	5	2	6	6	3	1
5.......	2	0	3	5	1	2
6.......	1	1	2	3	0	2
7.......	1	1	2	2	1	4
8.......	2	0	3	2	1	7
9.......	2	2	1	1	6	3
10.......	5	5	8	6	0	7
Total..	50	50	45	63	52	56

TABLE III. P_k, by Station

k	1a	1b	1c	2a	2b	2c
1.......	.356	.298	.469	.354	.302	.452
2.......	.150	.132	.155	.157	.159	.143
3.......	.107	.105	.097	.108	.117	.086
4.......	.084	.090	.069	.083	.096	.066
5.......	.069	.078	.052	.067	.079	.056
6.......	.058	.070	.042	.057	.066	.049
7.......	.051	.063	.035	.050	.056	.044
8.......	.045	.058	.030	.045	.048	.039
9.......	.041	.054	.027	.041	.041	.034
10.......	.038	.052	.024	.038	.036	.030

Judging from the values of P_1, which show for each area the proportion of all observed species revealed by a single sample, sampling efficiency is greatest in the riffles, second in the marginal areas, and poorest in the pools. Specifically, about 45 per cent of the observed species in the riffles, 35 per cent of those in the margins, and 30 per cent of those in the pools were taken in each sample, on the average. Table IV gives the average number and also the range of different species observed in single samples drawn from each location. The wide ranges of single sample recoveries reflect the random sampling employed in this study. Had the sample plots been carefully selected for potential fruitfulness, these ranges would doubtless have been much narrower.

The sum of the first three P_k values at each station shows that three samples yielded, on the

TABLE IV. Average Number and Range of Species Observed per Sample, by Station

Station	Average	Range
1a	17.8	12-30
1b	14.9	7-21
1c	21.1	13-29
2a	22.3	15-30
2b	15.7	0-27
2c	25.3	21-34

average, at least half and in some cases two-thirds of the species observed after ten samples. The average set of five samples yielded over 80 per cent of all observed species. In contrast, as many as 10-15 per cent of the species were not observed, on the average, until at least the eighth random sample had been collected.

The method used here supplies no information about the probability of observing a particular species in a given number of samples. However, we may argue that species discovered in early samples under similar environmental conditions are likely to be those found in almost every one of the ten study samples. On the other hand, species not revealed unless a large number of samples are taken, are represented chiefly by those found in only a few of the study samples. The numbers of individuals from common and rare species collected in each sample provided interesting clues to their distributions over the bottom areas.

For example, *Chironomus decorus* and *Physa integra* were found in at least eight of the ten samples taken at each sampling site. Except at Station 2c (riffle), both species showed great variation in numbers collected per sample, indicating strong tendencies to colonize in favorable habitats despite a tolerance to widely differing environments. Variation in numbers of *Chironomus decorus* was especially pronounced: collections ranging from less than ten to hundreds of individuals in the same bottom area. *Limnodrilus* sp. was also found throughout the sampling areas and was extremely abundant in pools. This annelid worm flourishes in the presence of organic pollution.

Other species were widespread but highly varying in numbers at certain stations or bottom types while rare or absent elsewhere. Examples were: (1) *Stictochironomus varius,* found in almost every marginal and riffle sample at both stations but almost entirely absent in pools, (2) *Callibaetis* sp., widespread in marginal areas at both stations but exceedingly rare or absent in pools and riffles, (3) *Dero* sp., widely distributed in all areas at Station 2 (clean water zone), but rare at Station 1 (recovery zone), (4) *Tubifex* sp., found in abundance at Station 1 and in pools at Station 2 (similar to *Limnodrilus*), but rarely seen in marginal or riffle areas in the clean water zone, (5) *Hydrobaenus* sp., frequently abundant in riffles at Station 1 but entirely absent from any other sampling area, and (6) the genus *Pristina,* represented by *Pr. longiseta, Pr. serpentina, Pristina* sp., or by all three, widespread in margins and riffles at Station 1 but seen in only a few samples at each of the other sampling sites. This genus was found in enormous numbers in the riffle samples.

All of these species conformed to the general rule that wherever a species was widespread and therefore well adapted to its environment, the members appeared to cluster in particularly favororable microhabitats. Thus, within the same marginal, pool, or riffle area, sample catches ranged from none or very few individuals to tens, hundreds, or even thousands. This can be attributed, in part, to the tendency of certain species to lay their eggs in masses rather than singly or in small dispersed groups.

In contrast, species detected in just occasional samples were usually represented by only one member per sample, seldom by more than three. Notable exceptions to this general finding were *Pristina longiseta* and *Pristina serpentina,* found in highly varying numbers even when present in no more than three samples at a station. However, as noted above, these species appeared abundant and widespread in other areas, so cannot be expected to have followed the same pattern as the rare species.

DISCUSSION

The results described above indicate the complex organization of invertebrate bottom fauna in Lytle Creek. In such streams, the bottom types to be sampled must be carefully selected since the labor and time involved in routine collection and taxonomic analysis of bottom samples demand that only a small number of samples be taken at any one time.

The standard sampling devices in use are not designed to collect effectively the small immature stages of larger organisms and the many species of smaller macroscopic forms which may border on the microscopic. If such smaller organisms are to be considered in a biological stream survey, special techniques must be used in their collection as well as in their subsequent handling. If use of these techniques is not planned, a limit should be set on the minimum size of the organisms to be considered in the study.

The extent to which these data from Lytle Creek are representative of other streams depends on similarities in size, ecological characteristics, and sampling methods used. Some streams are more uniform throughout their length, allowing more efficient sampling because the fauna is more uniformly dispersed and the number of suitable sampling areas not so limited. According to Needham (1938), small cold head-water streams less than seven feet in width are generally more productive per unit area than wider streams. Such streams exhibit less daily as well as seasonal fluctuation in volume and temperature and more ideal growing conditions for both insects and fish throughout the year.

Further study of various sampling techniques in different classes of streams is needed to determine the number of samples required in each case for a comprehensive faunal picture. Such information would provide a basis for reconciling the objectives of a biological stream survey with the staff, equipment, time and money available.

Finally, it should be emphasized that equation (1) is concerned only with those species which have been detected in the n study samples. It provides merely a short-cut method for anlyzing the sampling to reveal the average rapidity with which these species were recovered. No assumptions concerning the randomness of sampling or the distribution or relative abundances of the various species are required. Therefore, the formula is a convenient tool for the evaluation and comparison of different sampling techniques under a variety of environmental conditions. Perhaps its most useful application lies in the analysis of a pilot study, involving large numbers of carefully selected samples, on the basis of which a recommendation will be made of some smaller number for future routine surveys.

ACKNOWLEDGMENT

The authors wish to express their appreciation to Dr. C. M. Tarzwell of the Sanitary Engineering Center for his advice and assistance in planning this sampling study.

SUMMARY

1. A statistical method has been presented for determining the efficiency of ecological sampling, that is, the extent to which each successive sample has revealed the species observed at the end of a series of samples.

2. This method has been applied to macro-invertebrate fauna observed in sets of ten bottom samples randomly drawn from marginal, pool, and riffle area at two sampling stations on Lytle Creek, Ohio. Each area was sampled with equipment presently believed to be the most suitable for that area.

3. Species widespread in any given sampling area tended to vary greatly in their distribution over the area, clustering in favorable microhabitats. Many species, however, occurred in only occasional samples and were usually represented by a very few individuals. As many as 10-15 per cent of species were not discovered, on the average, until at least eight samples had been taken.

4. These results indicate the need for careful selection of the bottom types to be sampled in order that a small number of samples may give a comprehensive faunal picture. Further information on the adequacy of various sampling techniques in different classes of streams would be of great value in designing biological stream surveys.

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AN ECOLOGICAL STUDY OF THE PEREGRINE EARTHWORM *PHERETIMA HUPEIENSIS* IN THE EASTERN UNITED STATES[1]

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Pheretima hupeiensis, a megascolecid earthworm indigenous to the mainland of China, appeared in epidemic proportions of golf greens in Westchester County, New York, and Fairfield County, Connecticut, in 1948. A research project was initiated in 1952 in order to obtain further information on the biology of this peregrine species. The morphology of the worm has been reexamined and laboratory investigations of its moisture and temperature relationships have been reported by Grant (1955a, 1955b, 1956). For comparison two common lumbricid worms, *Eisenia foetida* and *Allolobophora caliginosa,* were frequently used in these studies. The present paper deals with certain ecological studies of the above three species of earthworms conducted in the laboratory and in the field.

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Ecological studies on earthworms have primarily been concerned with two major problems: the effect of the worms on the physical and chemical properties of the soil and the effect of such environmental factors as temperature, moisture, pH, etc. on the distribution and abundance of the animals. Little work has been done on life cycles and the possible interrelationships of species in the edaphon.

Soil which has passed through an earthworm's gut can be expected to have different chemical and physical properties from those of the original soil. Puh (1941) and Lunt and Jacobson (1944) found that the casts of lumbricid worms (probably *A. caliginosa*) had a higher content of organic matter, exchangeable calcium, potassium, etc. than the surrounding soil. There was also a tendency for the pH of the castings to approach neutrality. In *P. hupeiensis,* Schread (1952) found that the castings had a lower content of organic matter than the soil but the pH values were approximately the same. Whether or not worm activity actually increases the productivity of the soil is a matter of some controversy. Chadwick and Bradley (1948) concluded that although castings are beneficial when added directly to potted plants, the presence of large numbers of worms in cultivated areas has no beneficial results upon plant production. Russel (1910) felt that the chief influence of worms on productivity was through their physical cultivation of the soil rather than any chemical effect they might have on it.

A number of authors have estimated the rate at which worms till the soil by obtaining the weight of the castings thrown up on a uniform surface area over a period of time. Darwin (1881) estimated the annual turnover near Nice at 14.58 tons per acre. On fields of different agricultural history, Evans (1948) calculated the rate of casting to be from 1 to 25 tons per acre per year. Schread (1952) has given a value of 18.58 tons per year for *P. hupeiensis* on golf greens.

The comparative activity of some European species of earthworms has been described by Franz (1942). Worms were placed in glass vessels partially filled with white sand and fine clay underlying a layer of rich mor soil. *Octalasium studiosum* completely saturated the sand with humus within two months, while *Lumbricus polyphemus* restricted its activity to the humus layer. Evans (1947) observed the burrow systems of *Lumbricus rubellus, Lumbricus terrestris* and *Allolobophora caliginosa* in large, glass walled chambers filled with subsoil and intermediate and topsoil. As long as adequate food was available in the topsoil little burrowing occurred at the lower soil levels. The two species of *Lumbricus* deposited their castings at the surface, while *A. caliginosa* deposited excrement in its old burrows.

It is apparent that the site greatly affects the abundance of earthworms, their numbers being greatest in rich, well watered and aerated soils and least in acid mor or arid soils. Bornebusch (1930) found that the numbers of lumbricid worms varied from 177 per square meter in beech mull to 29 in impoverished beech mor soil. Kobayashi (1938) gives numbers from 1 to 110 per square meter for species of the genus Pheretima living in Korean sapling beds. In a study of the earthworms of Ohio, Olson (1928) found most worms in areas where the organic content of the soil was between 4 and 5 per cent, and the per cent moisture between 12 and 35. Dimo (1938) and Thompson (1924) have shown that continued plowing can cause considerable reduction in the earthworm populations of agricultural soils. Dimo maintains that this can be attributed to predation by birds which follow the plough, but Thompson more reasonably suggests that multiple factors are involved, such as the opening of the soil to greater fluctuations in moisture and temperature upon the removal of the turf. It is well known that the distribution of a species can often be correlated with a soil type. Bornebusch (1930) has confirmed that *Dendrobaena arborea* is most commonly found in rotting wood, while *Lumbricus terrestris* prefers pasture and garden soil. In light and medium loams Guild (1948) found *A. caliginosa* to be the dominant form. The abundance of *E. foetida* in compost and manure piles is well known.

The activity of worms in the soil is dependent on seasonal fluctuations in temperature and precipitation. Stockli (1928) describes the two periods of greatest earthworm activity as occurring in the early spring and fall. During the hottest summer months worms may burrow to deeper soil levels or go into diapause in earth capsules lined with mucus secretion. According to Evans and Guild (1947), *A. caliginosa* has a facultative and *Allolobophora longa* an obligatory diapause. Kobayashi (1938) found that in Korea, *P. hupeiensis* was present in the upper soil levels from June through September, but retreated to depths of 80 centimeters during the winter months.

The life cycles of earthworms are not well known. Evans and Guild (1948) have studied the life cycles of several species. *A. caliginosa* and *E. foetida* require an entire year to reach sexual maturity. The incubation period of the eggs varies with the season and species, but averages from 2 to 4 weeks for lumbricid worms. Oisha (1930) has described the life cycle of *Pheretima communissima* from Japan. Hatching occurs at the end of December and sexual maturity is reached by the following summer. The incubation of *Pheretima* cocoons is seldom less than eight weeks according to Bahl (1950). Kobayashi (1938) found that in Korea, mature individuals of *P. hupeiensis* were numerous from June through September, but were considerably reduced in numbers during the remaining months, none being recorded during October, November, and January.

Acknowledgment

The author wishes to express his appreciation to Dr. G. E. Pickford and Dr. Roger B. Friend for their interest and assistance throughout the present investigation, and to Prof. G. E. Hutchinson for much helpful advice. The portion of the work conducted at The Connecticut Agriculture Experiment Station was supported by a grant from the Westchester-Connecticut Turf Improvement Association.

Methods

Burrowing Activity. In order to study the burrowing activity of earthworms cages were constructed of glass plates separated by half-inch strips of wood at the bottom and sides and held in position with large Hoffman clamps. A layer of three-year-old humus was placed within the chamber over a layer of fine quartz sand. This type of chamber has proved very successful as it is not only light and manageable, but easy to construct. Strips of heavy rubber or glass would undoubtedly be more practical than wooden ones which frequently swell when the soil in the chamber is moistened.

The half-inch width of the container was narrow enough so that virtually all of the burrows made by the worms could be observed. For analysis of the total activity, the burrows were traced on large sheets of cellophane with India ink. The tracing from the back of the container was superimposed on that of the front. With the exception of a few cross connectives the entire burrow system was thus reconstructed. The total length of each system was measured in centimeters with a map distance meter.

Field Studies. Data on the abundance, vertical distribution and life cycle of *P. hupeiensis* were obtained from two-foot-square diggings made from June 1952 through April 1953 in the greens nursery plot of the Pelham County Club, Pelham, N. Y. The 0-6, 6-12, 12-18 inch soil levels were thoroughly examined for specimens of the worm and the numbers at each level recorded. Lumbricid worms occurring in the samples were also recorded. Using a standard soil thermometer the temperature at each level was recorded and large soil samples taken for estimation of the moisture content. During the months of July and August 1952, the pH at each level was determined.

Laboratory Studies

In the first series of experiments the soil chambers described above were utilized. A layer of barnyard manure was placed at the surface to a depth of about two inches. The manure, humus and sand levels were labeled L, A and B respectively to correspond to the litter, A and B horizons that were found in many soil profiles. Two mature specimens of *E. foetida, P. hupeiensis* and *A. caliginosa* were added to chambers 1, 2 and 3 respectively and the chambers placed in a constant temperature cabinet at 20°C. The appearance of these chambers at the end of a two-week period is shown in Figure 1.

Over a period of two weeks the specimens of *E. foetida* restricted their activity to the litter of manure. Considerable casting occurred in the litter but no definite system of burrows was observed. *P. hupeiensis* had tunneled extensively in the humus layer and had started a burrow system in the B horizon, filling large sections of the burrows with excrement. *A. caliginosa* constructed a few burrows in the sand, but remained largely in the humus layer.

The chambers were examined again in two weeks. After a total period of four weeks, the specimens of *E. foetida* were still located in the manure which had by now been so thoroughly worked over that a major portion of it must have passed through the guts of the animals. Worms of this species were occasionally found with the posterior third of their bodies extending into the humus, but none were observed to have penetrated the lower horizons by active burrowing. In the case of *P. hupeiensis* the humus layer was by now entirely composed of aggregates of castings. No definite burrows could be identified at this level. The burrow system of the sand level was considerably extended

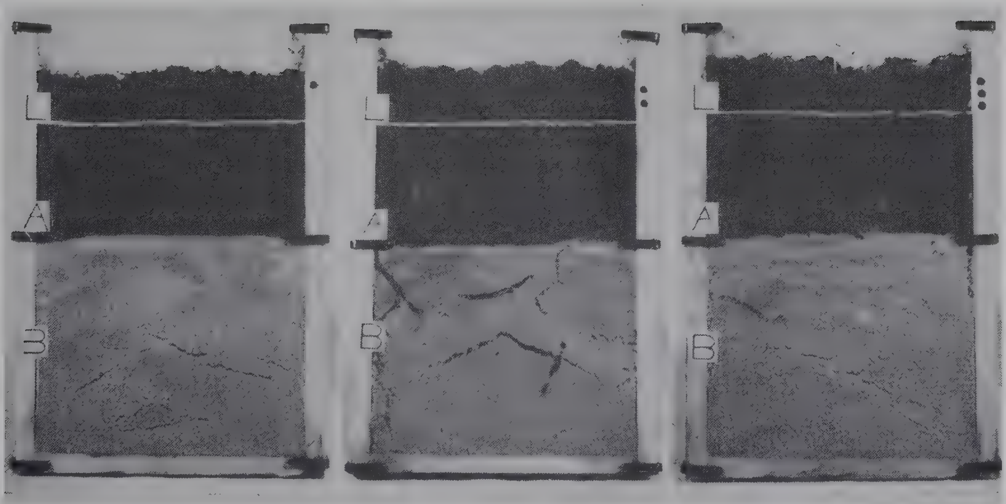

FIG. 1. Appearance of soil chambers kept at 20°C at the end of a two week period. Specimens of *E. foetida* which were placed in the first chamber on the left confined their activity to the litter layer (L). In the next two chambers to the right which contained specimens of *P. hupeiensis* and *A. caliginosa* respectively, burrowing occurred in the humus layer (A) and in the sand layer (B) where castings of humus material deposited in the burrows can be observed.

and the majority of the burrows were packed with excrement. The worms were never observed at the surface, nor was there any evidence of surface casting. The original burrows made by *A. caliginosa* in the humus had been obliterated and replaced by a new burrow system. Considerable subsurface casting was noted at this level and much surface casting had taken place within the litter material. In the sand level new burrows had been constructed and partially filled with humus. The appearance of the chambers containing *P. hupeiensis* and *A. caliginosa* after a four week period is shown in Figure 2. Reconstructions of the burrow systems of the two species are shown in Figure 3. Because of the extensive activity it was not possible to reconstruct a system of burrows for *P. hupeiensis* in the humus layer, and indeed it is probable that no definite systems were ever constructed here. The burrows constructed by *A. caliginosa* in the humus layer largely represent those constructed during the last two weeks of the experiment, as many of the original burrows had been obliterated.

The burrow system of *P. hupeiensis* in the B horizon measured 186 centimeters in length and was filled with excrement for 50.5 per cent of its total length. That of *A. caliginosa* was 59 centimeters long and was 50.8 per cent filled with castings. Thus under the conditions of the above experiment *P. hupeiensis* was most effective in enriching subsoils. Although no precise measurements were obtainable, there is indication that the total burrowing activity in both the A and B horizons was greater in *P. hupeiensis* as this species had completely worked over the topsoil whereas *A. caliginosa* had merely constructed several series of burrows.

There was considerable difference in the shape of the burrows of *A. caliginosa* and *P. hupeiensis*. Whereas the former constructed a series of interconnecting burrows roughly U-shaped in form, the burrows of the latter were of a less well defined pattern with numerous anastamosing branches. It is probable that the burrows made by *P. hupeiensis* do not constitute a permanent system at all. The animals were frequently observed casting directly into a burrow which was in the process of formation.

A. caliginosa always kept an occupied burrow free of castings, and deposited castings only in areas no longer in use.

A second series of experiments was performed on *P. hupeiensis* to determine the effect of temperature on burrowing activity. Three chambers were constructed and each was partitioned into two columns. Six inches of quartz sand were placed in each column and covered with a six-inch layer of humus. A single worm was then placed in each column, and the chambers placed in constant temperature cabinets at 10°, 20° and 24°C. Reconstructions of these burrow systems are shown in Figure 4. Table I gives the lengths of each system and the percentage of its length filled with castings. The greatest activity occurred at

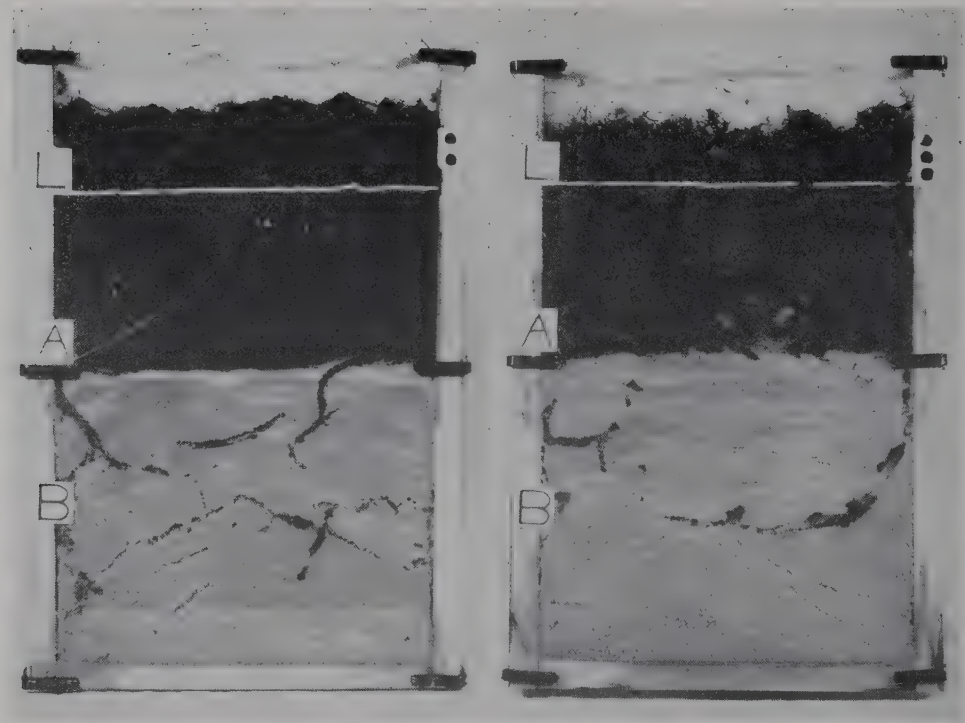

FIG. 2. Soil chambers at the end of a four-week period. The chamber containing specimens of *P. hupeiensis* is on the left and that containing specimens of *A. caliginosa* on the right.

TABLE I. Comparative lengths of the subsoil burrow systems and the percentage of the burrows filled with castings for specimens of *P. hupeiensis* kept at different environmental temperatures

Test temperature	Specimen no.	Length of burrow, cm.	Percentage filled with castings
10° C	1	5	50.0
	2	20	55.5
20° C	1	69	76.8
	2	62	82.2
24° C	1	16	36.3
	2	13	38.2

20°C and the least at 10°C. In the chamber kept at 20°C the humus had been completely worked over, while in the chambers kept at 10° and 24°C only a few burrows were constructed. It is interesting to note that not only was the total burrow length of the sand horizon greater in the column kept at 20°C, but that the percentage of the burrow filled with castings was greater as well. At 10°C all of the burrowing activity occurred during the first day, the worms remaining quiescent in the humus layer during the remainder of the experiment. At 24°C the burrows contained a low percentage of castings, and it seems likely that feeding as well as burrowing capacity is impaired at higher temperatures. Worms used in the above experiments had been acclimated at a temperature of 20°C.

In a brief experiment *A. caliginosa* and *P. hupeiensis* were placed in liter cylinders filled with a six-inch layer of sand over a humus layer of corresponding depth, thus reversing the procedure of the previous experiments. At the end of two weeks *P. hupeiensis* had constructed numerous burrows in the sand and humus, whereas *A. caliginosa* had kept entirely to the humus level. When tap water was introduced at the base of the column until a water table had formed at the sand-humus interface, *A. caliginosa* withdrew from the submerged humus layer within twelve hours. When the water table was elevated the worms were driven to the surface of the column. Although driven up by a rising water table, specimens of *P. hupeiensis* returned to submerged levels for short periods of time, and were general-

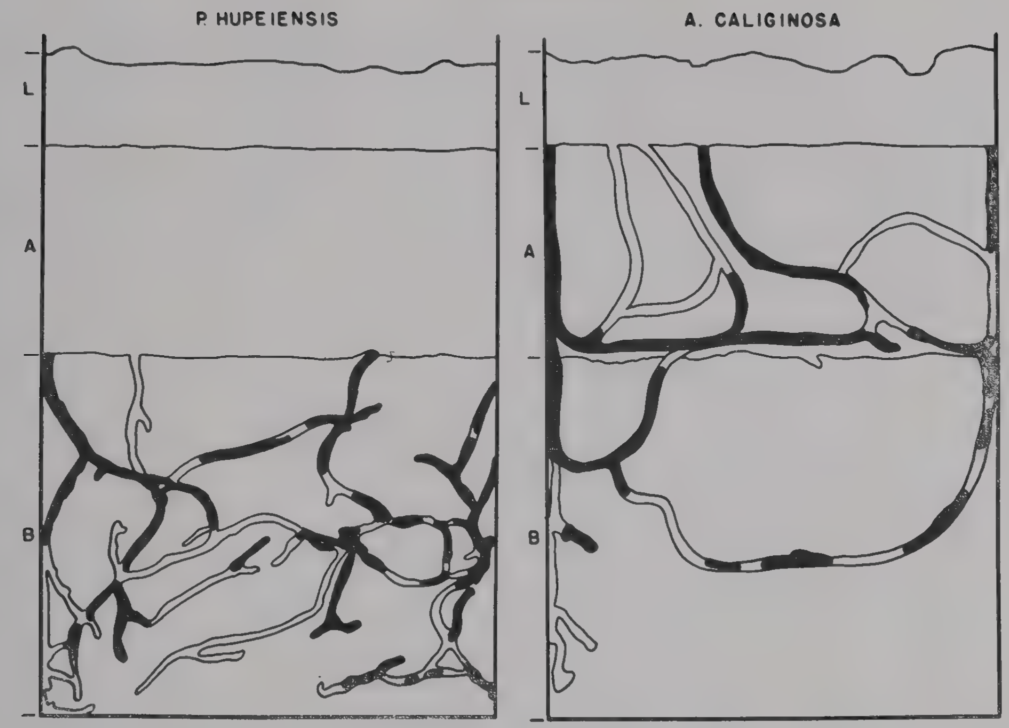

FIG. 3. Reconstruction of the burrow systems of *P. hupeiensis* and *A. caliginosa* in the B horizon. Solid areas represent burrows filled with castings. The burrow system of *A. caliginosa* in the A horizon is also indicated.

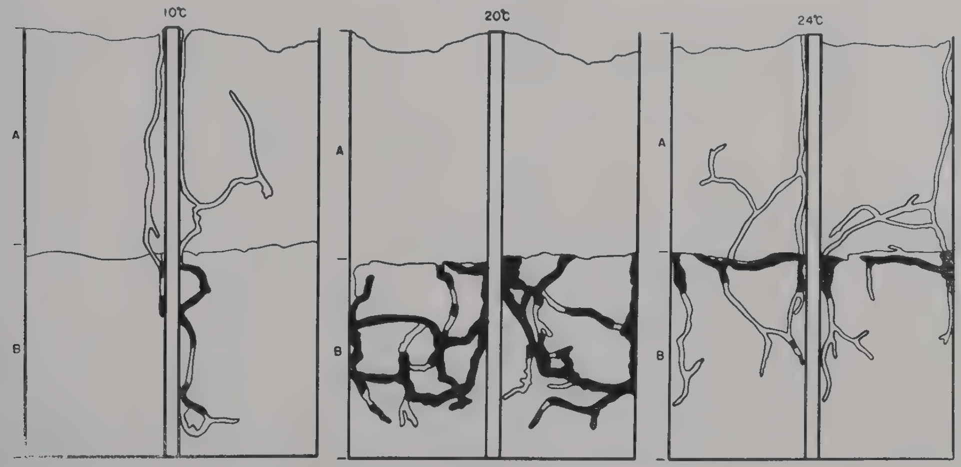

FIG. 4. Reconstruction of the burrow systems made by *P. hupeiensis* at 10°, 20°, and 24°C.

ly active at the water-air interface. A tendency for worms of this species to orient with their posterior ends away from the submerged areas was apparent. When the water table was extended into the sand layer, *P. hupeiensis* cast humus from submerged levels at the surface of the column. If the entire column was flooded, sorties for food to deeper levels were greatly diminished and the worms themselves appeared at the surface for periods of time.

FIELD STUDIES

Abundance. A careful count was made of the numbers of *P. hupeiensis* collected from two-foot-square plots from June 1952 through April 1953. *P. hupeiensis* was the only earthworm present in reasonably large numbers at any time. Estimates of numbers from the collections made from June through September give values of 87-122 per square meter. It was impossible to obtain an accurate estimate of population numbers during the winter months as most worms retreated to deep soil levels beneath heavy gravel and rock.

All worms were collected from a section of a greens nursery plot which had been under sod for at least ten years. According to Schread (1952) the soil of this area varies from loam to sandy loam. Soil analyses show that the percentage of organic matter in the soil is relatively high down to the 12 inch level. The pH at all soil levels is about 6.0. Compared to a rich botanical humus the values for nitrate, nitrogen, ammonia nitrogen and potassium are low, while phosphorus is medium. Calcium is abundant in the upper six inches, but low at greater depths. Magnesium is high in the upper 18 inches. It is interesting to note that in a section of the nursery plot recently ploughed no lumbricid worms were taken and the numbers of *P. hupeiensis* were so small as not to warrant further study.

Vertical Distribution. The distribution of *P. hupeiensis* and various lumbricid earthworms at different soil levels from June 1952 through April 1953 is shown in Table II, as well as the temperature and the moisture percentage at each level. *P. hupeiensis* was active during the summer months in the 6-18 inch soil levels usually in the region of the greatest moisture content. During August large numbers of worms were taken in the 6-12 inch horizon, where moisture content was less than at the surface. This can be explained by the fact that an early morning rain had temporarily soaked the upper levels. In September worms were generally found near the surface, but by October when temperature had fallen to 12°C at the surface, the majority of the animals were found in the 16-18 inch levels where temperatures were slightly higher. During the winter months most worms penetrated to depths of 22 inches or more. In March, following heavy rains, the animals were active in the upper six inches of soil at temperatures of about 10°C.

A. caliginosa, the only other worm found in any numbers, remained at higher levels in the soil throughout the year than did *P. hupeiensis.* During an extended drought in July several specimens were found enclosed in earth capsules at a depth of 5 inches. In the winter months this species was found deeper in the soil, but not until February had most individuals retreated below the 22-inch level. The fact that so few lumbricid worms were taken from the nursery plot was probably due to the use of vermicides, such as arsenate of lead, in this area over a period of years. According to Fleming and Hadley (1945) such measures are ineffective in controlling *P. hupeiensis.*

TABLE II. Records of the vertical distribution of *Pheretima hupeiensis* and the common lumbricid worms *Allolobophora caliginosa* and *A. chlorotica* and *Lumbricus terrestris* at Pelham, New York, from June 1952 through April 1953. E = worms enclosed in earth capsules. Per cent moisture is based upon the oven-dry weight of the soil

Date	Inch Level	A caliginosa	A. chlorotica	L. terrestris	P. hupeiensis	Temp. °C	Moisture percent.
June 16	1-6	5	2	0	0	23.3	14.2
	6-12	0	0	0	28	21.6	18.2
	12-18	0	0	0	3	20.0	15.5
July 10	1-6	4, 2E	4E	0	0	23.3	15.1
	6-12	1E	0	0	8	22.2	13.2
	12-18	0	0	3	27	20.5	15.6
Aug. 13	1-6	5	1	0	1	26.8	21.6
	6-12	9	0	0	34	23.3	16.4
	12-18	0	0	1	9	22.7	15.5
Sept. 3	1-6	10	6	2	29	21.6	22.6
	6-12	1	0	1	18	22.7	20.8
	12-18	0	0	0	0	22.2	21.5
Oct. 9	1-6	8	3	1	2	12.7	20.7
	6-12	0	0	1	16	13.3	19.4
	12-18	0	0	0	11	15.5	18.3
Nov. 11	1-6	1	0	0	0	4.4	20.1
	6-12	6	0	0	0	5.0	20.6
	12-18	1	0	1	0	6.1	21.7
	18-22	0	0	0	9	6.1	19.1
Dec. 15	1-6	0	0	0	0	1.6	25.1
	6-12	0	0	0	0	2.7	23.3
	12-18	5	0	0	0	3.8	24.2
	18-22	0	0	2	3	4.1	21.8
Jan. 6	1-6	0	0	0	0	3.3	29.3
	6-12	1	0	0	0	4.4	30.1
	12-18	4	0	1	0	5.9	31.7
	18-22	0	0	0	3	5.4	28.4
Feb. 23	1-6	0	0	0	0	Frozen	28.1
	6-12	0	0	0	0	.56	28.2
	12-18	0	0	0	0	2.7	29.6
	18-22	1	0	0	4	3.5	25.9
Mar. 20	1-6	4	2	0	31	10.1	32.8
	6-12	2	0	2	9	11.9	30.2
	12-18	0	0	0	0	11.8	28.4
April 9	1-6	7	0	0	18	14.7	33.4
	6-12	0	0	0	3	15.3	30.7
	12-18	0	0	0	0	14.9	29.1

Life Cycle. The total number of *P. hupeiensis* collected each month was separated into juvenile, immature, semi-mature and mature categories and the number in each group recorded. The fre-

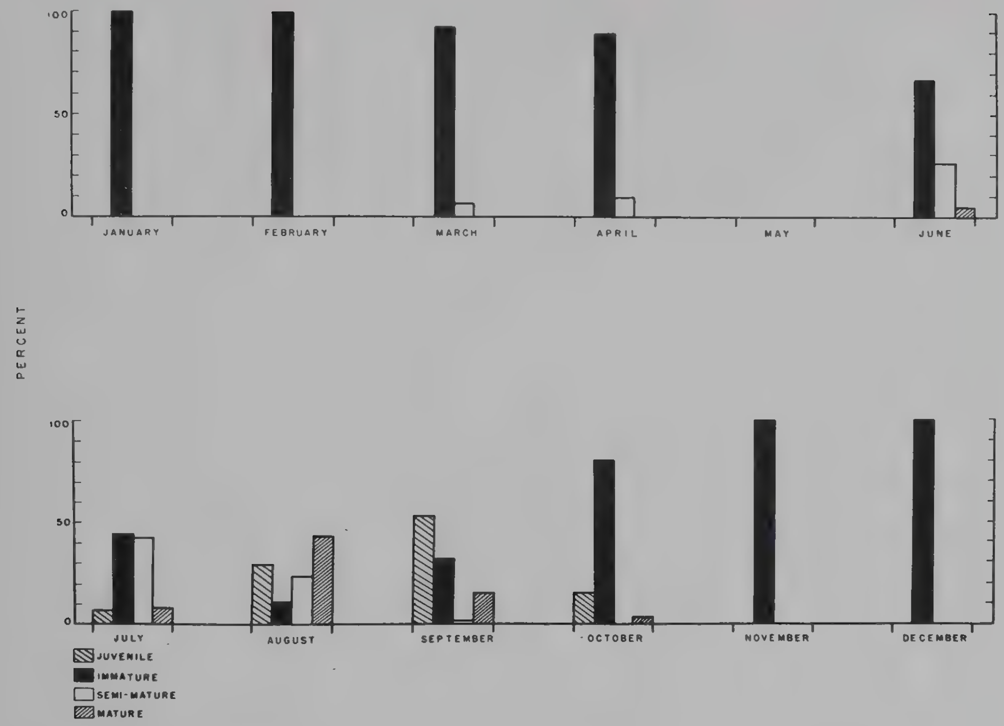

FIG. 5. Changes in the percentage distribution of the four categories of maturity indicated above, which occurred in samples of the *P. hupeiensis* population at Pelham, N. Y. from June 1952 through April 1953.

quency distribution of the four age categories is given in Figure 5. Although few specimens were available during the winter months because of their deep penetration of the soil, it may be assumed that the entire population was immature as these were the only types of individuals taken in the field at this time. In the laboratory cultures all specimens remained immature during the winter. By March and April a few semi-mature individuals were taken in the field. Through June and July the percentage of mature individuals increased reaching a peak in August, while the numbers of immature decreased as individuals of this category became sexually mature. The transitional semi-matures were most prominent during July and by September all such individuals had reached maturity. Juveniles first appeared during July and reached their maximum concentration in September. By October they were on the decline as most individuals had by now passed into the immature category. Juveniles kept in the laboratory became immature during October and remained in this state throughout the winter. It seems probable that *P. hupeiensis* has an annual life cycle with large numbers of mature individuals dying following reproduction. In the laboratory only one mature individual lived as late as December. Unfortunately no cocoons were found, nor was copulation or cocoon deposition observed, although large numbers of worms were kept under observation in the laboratory.

DISCUSSION

Records made in the field indicate that temperature and moisture conditions are important factors in the distribution of *P. hupeiensis.* In general it can be said that the worm avoids temperature extremes and is commonly associated with soil levels where the moisture content is high. These studies confirm the laboratory investigations on moisture and temperature reported by Grant (1955a, 1955b). During the summer months the animals are operative at soil levels where temperatures are between 22° and 23°C. These temperatures are at the upper limit of the laboratory preferendum of 15-23°C for worms conditioned at 20°C. The fact that a few worms were found in soil at 24°C may indicate a slight upward shift in the preferendum due to the modifying effect of soil moisture or the conditioning effects of temperature. The laboratory studies showed a 0.3°C rise in thermal tolerance for every 1°C rise in conditioning temperature. It is reasonable to assume that in summer soils worms have been conditioned at slightly higher temperatures than the 20°C used in the laboratory.

During the winter months, low temperatures cause the worms to seek the deeper, warmer soil levels. *P. hupeiensis* was not taken in the upper soil levels at this time although the moisture content was frequently higher than at lower levels. Laboratory experiments indicate that worms conditioned at 20°C are inactive in soils at 10°C. It is likely that Kobayashi (1938) is correct in his assumption that *P. hupeiensis* not only remains deep in the soil during the winter, but is in a state of hibernation as well. It is of extreme interest to note that in the field the species became active during March, appearing in the upper soil at temperatures of about 10°C. It seems certain that a lowering of the thermal resistance occurred during the winter months so that at the end of the winter worms were activated at temperatures which had previously caused retreat to warmer levels and complete cessation of activity in the laboratory. Schread (1952) reported that considerable surface activity occurred during a week in February 1949. This was due to a period of unusually high temperatures and precipitation.

The genus *Pheretima* is essentially tropical, occurring in Southeast Asia and Malaya, but *P. hupeiensis* is largely restricted to the more temperate zones of northern China and Korea. In the eastern United States its extreme northern limit has been Fairfield County, Connecticut, but it is probable that in the absence of the rigid controls now being applied, it would soon spread throughout New England. Unfortunately, we know nothing about the temperature tolerances of tropical species of the genus, but the tendency of *P. hupeiensis* to extend its range in a northerly direction may be the result of its low thermal tolerances which do not adapt it for tropical regions. In the areas where the species occurs the soils are usually quite moist and seasonal changes in temperatures are transferred to the depths of the soil at a slow rate and are never excessive. For example, the mean January temperatures in Korea are about −5°C and those of June 24.7°C, with an annual precipitation of 46.60 inches. In Fairfield County, Connecticut, the mean monthly temperatures for January and July are −1.4°C, and 22.7°C respectively and the annual precipitation averages 46.36 inches.

A. caliginosa, which has a higher thermal death point, a wider temperature preferendum and is more resistant to desiccation than *P. hupeiensis,* was found in the upper soil levels most of the year. Michon (1949) and Evans and Guild (1948) have shown that *A. caliginosa* has a facultative diapause in dry soils where it is found coiled within mucus-lined earth capsules which are resistant to desiccation. The fact that a few worms were found encapsulated during a period of drought in July 1952 at Pelham, N. Y. while others were found free in the soil, suggests that an extended diapause is not realized in moist, temperate soils, but only occurs in arid regions such as those described by Dimo (1938) where soil moisture falls below the hygroscopic coefficient to depths of 100 centimeters.

In the laboratory *P. hupeiensis* is very active in mixing topsoil with subsoil. *A. caliginosa* is generally less active and is found most frequently in rich topsoil. The former species is a sub-surface caster, while the latter may cast in the soil or on the surface. However, Schread found large quantities of castings of *P. hupeiensis* on the surface of golf greens in 1949 at Pelham. It is likely that in such localities where the soil is being continually watered the worms are driven to the surface, particularly after heavy rains. In the laboratory *P. hupeiensis* can be induced to cast on the surface of the soil if their container is flooded. Nagano (1934) indicates that such a reaction may be due to the high CO_2 content of water-logged soils. Drainage at the Pelham Country Club is very slow, so that after heavy rains many of the greens and large areas of the fairways are flooded. During the present study the only surface castings were observed in a flooded area of the greens nursery plot following a heavy rain.

The chemical effects of worms on the soil have been studied by a number of authors primarily by comparing the constitution of casts with that of the surrounding soil. In lumbricid worms the excrement is usually higher in available nutrients than the soil. However, Schread (1952) has shown that the castings of *P. hupeiensis* are poor in quality compared to those of the lumbricids. This may be due to the fact that the species does not feed in the rich topsoils as do the lumbricidae and apparently never feeds on undecomposed organic matter. In the laboratory *P. hupeiensis* refused to eat leaves, grass, raw vegetable matter, coffee grounds and bacon fat, all of which are readily accepted by *A. caliginosa* and *L. terrestis.*

E. foetida, which was used in a number of comparative laboratory tests, has temperature and moisture relationships approximating those of *P. hupeiensis.* Its distribution is confined to compost and manure. In the laboratory the species refused to burrow in rich humus if manure was available at the surface and would not penetrate into sand under any conditions. In nature the species is found near the periphery of manure piles where temperatures are moderate and moisture high. It is interesting to note that this species of worm, which is unable to survive in loamy soils, is the species most commonly cultured and sold to the organic gardeners.

As the soil is an amazingly complex and heterogeneous environment it is extremely difficult to define the precise habitat of a soil organism. However, it is quite apparent that species of earthworms found in a soil locality occupy different segments of the environment, and it is not surprising to find considerable differences in the physiological tolerances and behavior of each species. Thus *L. terrestris* feeds upon surface litter and lives in a permanent U-shaped burrow, down which the worm can retreat following unfavorable shifts in the upper soil environment. *A. caliginosa* inhabits topsoils where it feeds upon organic debris. When soil moisture is decreased it may go into a state of diapause or move to moister soil levels. Its castings are deposited on the surface or in its semi-permanent U-shaped burrow systems. *P. hupeiensis* on the other hand is generally confined to deeper soil levels and never casts upon the surface unless the soil is flooded. Its burrow systems, which are not of a permanent nature, are filled with subsurface castings. Evans (1947) suggests that the simple U-shaped burrows of *L. terrestris* may be comparable to those of the marine polychaetes and that the semi-permanent systems of *A. caliginosa* show a later deviation from the ancestral pattern. If this is the case, it is most interesting that *P. hupeiensis* shows a further modified burrow system as it belongs to one of the most advanced genera of the Oligochaeta. It is not possible to evaluate the behavior of *E. foetida* in this respect as it lives in a loose matrix where burrows as such are not required.

The present observations and those of Kobayashi (1938) indicate that *P. hupeiensis* has an annual life cycle. The actual conditions that bring on sexual maturity in the spring are not known. However, specimens in the laboratory which were placed at 10°, 15°, and 22°C during May and June all became mature after wintering at 20°C. Thus it is not likely that the warming of soils in the spring can alone be responsible for bringing about sexual maturity. It may be that any change of temperature following wintering at relatively standard temperatures may act as a trigger mechanism for maturation. It may be assumed that, as in the lumbricid worms reported by Avel (1929), sexual maturity in *P. hupeiensis* is also dependent on proper nutritional factors.

In conclusion it should be noted that the present work as well as that of many other investigators has demonstrated the vast differences between species of earthworms with regards to their effect upon soil conditions and the effect of the soil upon them. Thus the importance of proper specific identification of the earthworms in any study of the soil fauna cannot be over-emphasized.

SUMMARY

The burrowing activity of three species of earthworms was studied in the laboratory. In glass soil chambers, *E. foetida* remained in the surface litter of manure. *A. caliginosa* was active in the humus layer and made occasional burrows in the lower levels of quartz sand, depositing its excrement on or below the surface. *P. hupeiensis,* a peregrine megascolecid earthworm, made extensive burrow systems in both the sand and humus layers and deposited large amounts of castings in the sand. The effect of temperature on burrowing activity was studied on *P. hupeiensis.* In soil chambers kept at 10°C, 20°C and 24°C the greatest activity occurred at 20°C, which is a temperature well within the thermal preferendum of the species. In the 10°C chamber the worms soon became quiescent and appeared to be in a state of hibernation. *P. hupeiensis,* which is normally a subsurface caster, can be induced to cast on the surface if the soil in which it is kept is allowed to become waterlogged.

In a greens' nursery plot at Pelham, New York, the numbers of *P. hupeiensis* were estimated at 87 to 122 individuals per square meter. As few lumbricid worms were taken in this area it is assumed that they had been eradicated by vermicides which did not affect the *Pheretima* population. The vertical distribution of the earthworms in the area was recorded from June 1952 through April 1953 at specific soil levels together with the temperature and per cent moisture at each level. During the summer months *P. hupeiensis* was active in the 6-to-8-inch soil levels and was active near the surface only in September and March when temperatures were low and moisture was high. From November to February the worms had retreated to deeper, warmer soils below the 22 inch level. The few specimens of *A. caliginosa* recorded were found near the surface until December when low temperatures caused their withdrawal to deeper soils. There is an indication that *P. hupeiensis* has an annual life cycle. Mature individuals are abundant in August and die following reproduction. Juveniles are numerous in September, but by November the entire population has become immature and remains in this state throughout the winter months.

The ecological studies support previous laboratory investigations into the temperature and moisture relationships of earthworms. Species of worms, even those found within a single soil area, occupy different segments of the environment which are defined by the reaction of the worms to such factors as temperature and moisture. Hence the extreme importance of species identification in studies of soil fauna is indicated.

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RELATIVE AMOUNTS OF VITAMIN B_{12} IN DETRITUS FROM OCEANIC AND ESTUARINE ENVIRONMENTS NEAR SAPELO ISLAND, GEORGIA[1]

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INTRODUCTION

The area in the vicinity of Sapelo Island, Georgia represents a unique estuarine environment. The island is separated from the mainland by approximately 9 km of extensive salt marsh in which *Spartina alterniflora* is the dominant plant and which contains an elaborate drainage system accessible to the open ocean. Tide levels may at times exceed 280 cm. Periodically, the marshes are inundated and subsequently drained as a result of tidal action. During the course of this flushing process, there is undoubtedly an exchange of soluble and insoluble nutrients between the marshes and the waters which are biologically very productive. The waters support varied populations of microorganisms, shrimp, oyster, crab, and fish. In addition tidal movements aid in the exchange, transport, and relocation of the suspended matter or detritus[3] between the water and the marsh. It is a process which directly affects the general ecology of the region.

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The distribution of vitamin B_{12} in the detritus was investigated using microbiological assay procedures. Vitamin B_{12} was selected for initial studies as it is produced in quantity by many microorganisms (Robbins, Hervey, and Stebbins 1950). Lochhead and Thexton (1951) demonstrated that 70-84 per cent of the bacteria isolated from soil were cobalamin producers. Vitamin B_{12} represents, also, an essential factor for the growth and development of other microorganisms (Provasoli and Pintner 1953) which in turn are an essential part of the food network extending through the marine invertebrates, vertebrates, and in some cases to man. Oysters and clams were found to contain large amounts of cobalamin (Robbins *et al.* 1951) suggesting that the flagellates which are an important part of their diet are either producers or accumulators of vitamin B_{12} (Provasoli and Pintner 1953).

Studies of the nutritional requirements of marine microorganisms in culture indicate the essential nature of vitamin B_{12} for growth and development of many algal phototrophs (Hutner and Provasoli 1951) which play an important role in the fertility of the ocean. Marine dinoflagellates which were grown in pure culture required vitamin B_{12} (Sweeney 1954). A marine *Stichococcus* sp. was found to require a growth factor present in natural sea water which could be replaced by crystalline vitamin B_{12} (Lewin 1954). The studies of Wilson and Collier (1955) on the nutritional requirements of *Gymnodimium splendens* and *G. brevis* Davis showed that vitamin B_{12} and other unknown growth factors were essential for growth. Droop (1955) studied a bacteria-free culture of *Skeletonema costatum* and demonstrated a cobalamin requirement. A comprehensive table with references on the vitamin B_{12} growth requirements of microorganisms was compiled by Ford and Hutner (1955). In addition they described relationships within the B_{12} family of compounds and discussed the role of these compounds in the metabolism of microorganisms. Other reviews have been published by Jukes and Stokstad (1951), Shive (1951), and Jukes *et al.* (1954). The nutritional role of vitamin B_{12} is reviewed by Hutner and Provasoli (1954), and its function in the metabolism of nucleic acids is reviewed by McNutt (1952).

It is felt that a knowledge of the vitamin cycles of estuarine and oceanic environments will increase our understanding of the fertility of the ocean and perhaps serve as a practical guide for the future farming of the ocean. Studies such as those described in this paper may aid in the prediction of algal blooms and hence serve the investigator as an additional tool for study of ecological succession.

The author wishes to express his thanks to Dr. and Mrs. P. R. Burkholder for performing the microbiological assays.

PROCEDURES

Description of sampling areas. Samples of water were collected at designated stations representing a line approximately 30 km in length. The stations extended (Fig. 1) from the offshore ocean waters (Stations 1-5), through Doboy Sound (Stations 6-9), and along the length of the Duplin River (Stations 10-17). The waters of the Duplin River and its tributaries flow through rich salt marsh which supports an abundance of *Spartina alterniflora.* It is a dead tidal bay and has no outlet other than Doboy Sound. The movement of the river varies as the tide rises and falls. Doboy Sound is a mixing basin located south of Sapelo Island and receives the waters of many tributaries which drain the surrounding marshy regions. In addition it receives some of the fresh water of the Altamaha River which flows through a large section of Georgia. The waters of the sound are usually muddy during the flood and ebb tides and flow into the open ocean as shown in Figure 1.

Collection of samples and tidal relations. The first station was established approximately 10 km southeast of Sapelo Island. Consecutively numbered samples were collected at different stations during the height of the flood tide and part of the ebb tide. The tide record which is shown in Figure 2 was taken at station 10 (see Fig. 1) with a recording gauge. The record was corrected to the low-tide level for the day and shows the time each sample was obtained in relation to tide levels at station 10.

For purposes of comparison with later experiments and because of the importance of tidal action on the movement of detritus, it should be noted that Figure 2 also shows the relative period of collection in relation to the flood and ebb tides at

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[3] Suspended matter or detritus refers to that part of a water sample retained by a millipore filter (AA, white, plain, .047 mm).

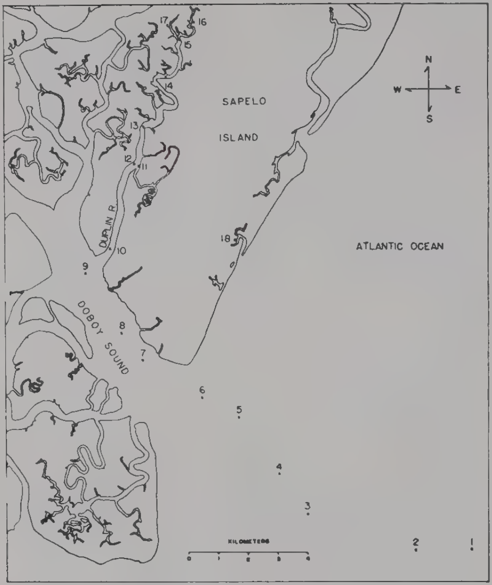

FIG. 1. Location of collecting stations and the vicinity of Sapelo Island, Georgia.

each station. Thus, the first eight samples were collected within a period of 35-45 min in the direction of the flood tide; slack high-water actually was observed to occur between the establishment of stations 8 and 9 and not at station 3 as shown in Figure 2; and the remaining samples 10-17 were obtained within a period of 30-40 min as the tide was ebbing and represented waters which had recently drained from the marsh.

Actually, samples 1-17 were collected within a period of 3 hr and 46 min but in relation to the tidal cycle, the relative period of collection represented that small part of the tide curve shown as the solid line in Figure 2 (*i.e.* the solid line between stations 1 and 5).

Station 17 which was located in the west branch at the north end of the Duplin River (Fig. 1) was selected for further study. A series of 12 water samples (A-L) were collected at this station over the course of a tidal cycle. Figure 3 indicates the time each sample was obtained in relation to the low-tide level for the day. The tide record was made with a staff gauge located at the station. It should be noted that the range of the tide was similar to that shown in Figure 2.

In other experiments, mud samples were obtained at stations along the length of the Duplin River. For comparison samples of muds and sediments were collected at station 18 (Fig. 1) which is a relatively sandy region devoid of marsh.

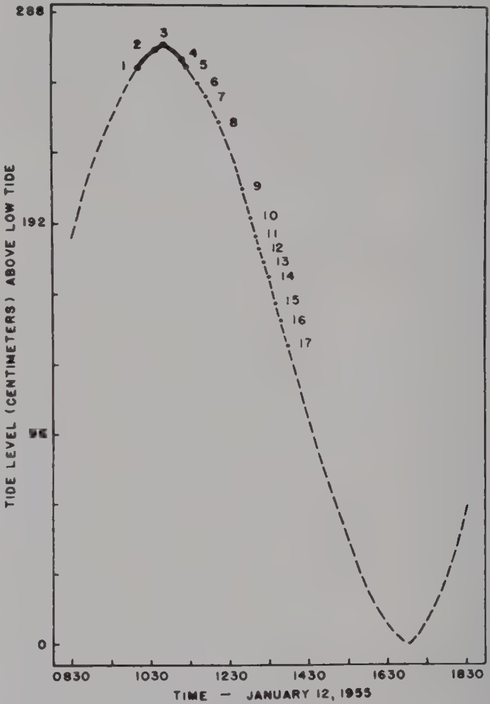

FIG. 2. Location of stations 1-17 in relation to tide levels recorded at station 10. Solid line between stations 1 and 5 represents actual tidal period for collection of all 17 samples.

Preparation of samples before microbiological assay. Surface water samples were collected in gallon jugs. As soon as possible after collection (1-3 hr), aliquots of 250 to 2000 ml depending on the turbidity of the sample were filtered by suction through tarred millipore filters. The filter pads were then dried in an oven at 100° C for 8 to 10 hr and weighed. For the calculation of the final weight of each detritus sample, a standard curve was prepared relating the initial weight of the pads to the weight gained after passing a filtrate through them. This procedure was necessary since pads which initially weighed 50 to 82 mg gained 4.3 to 6.2 mg respectively after the passage of a filtrate through them. As the salinity difference was small, 28 to 34 $^0/_{00}$, the variation of this factor was not considered further in the final calculation of the true weight of each detritus sample.

Microbiological assay. Assays for vitamin B_{12} were performed with a mutant strain of *Escherichia coli* 113-3 which was obtained originally from Dr. Bernard D. Davis. The methods of assay were essentially those described by Burk-

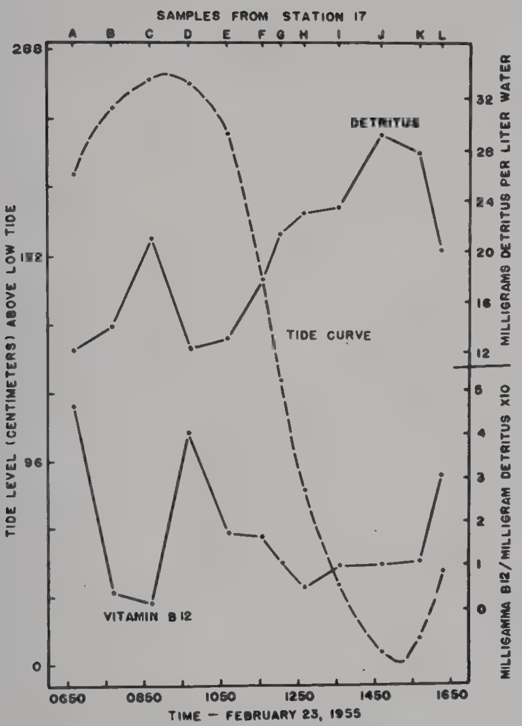

FIG. 3. Detritus loads of samples A-L collected at station 17 and the vitamin B_{12} content of the detritus in relation to tidal cycle.

holder (1951). The basal medium had the following composition per liter of double strength solution: K_2HPO_4, 14.0 g; KH_2PO_4, 6.0 g; Na citrate $\cdot 2H_2O$, 1.0 g; $MgSO_4 \cdot 7H_2O$, 0.2 g; $(NH_4)_2SO_4$, 4.0 g; glucose, 20.0 g; asparagine, 8.0 g; Na thioglycolate, 200 mg; and 50 mg each of arginine, glycine, glutamic acid, histidine, proline, and tryptophan. The pH was adjusted to 6.8. Vitamin B_{12} or samples and sufficient water to bring the volume to 2.5 ml were dispensed into clean culture tubes and the basal medium (X2) was added in the amount of 2.5 ml per tube. After autoclaving at 116° C for 5 min, the tubes were cooled and inoculated.

Inoculum was prepared by growing *E. coli* in Difco nutrient broth for 12 hr, washing once with physiological saline, and resuspending in saline. The tubes were inoculated with one drop of cell suspension per tube. They were incubated at 30° C on a slow rotary shaker for 18 hr. Growth was measured turbidimetrically with a Klett-Summerson colorimeter.

Preparation of the samples of mud and of the detritus filtered from the water samples was accomplished by suspending the material in buffer solution at pH 5.0. The samples were stirred and boiled for 10 min to release free vitamin into solution. It was found convenient to cut each cellulose-acetate filter with its adhering dried detritus into shreds and place the shreds of a single filter into 10 ml of buffer solution. After centrifugation, the supernatant was used in aliquots of 0.1 to 2.0 ml per assay tube.

Tests for methionine in the detritus samples using the *E. coli* mutant sensitive to methionine but not to vitamin B_{12} indicated no interference by methionine in our vitamin assays with *E. coli.*

Vitamin B_{12} as used in this paper refers to the family of B_{12} compounds. It is recognized that the pretreatment of the detritus samples before assay could have destroyed some B_{12} activity for the *E. coli* mutant used in this study. However, *E. coli* has the broadest specificity for the many forms of B_{12} found in nature. It responds to Factor B and to all the known pseudo-B_{12} compounds. It is possible that even if B_{12} were broken down appreciably with dry heat, *E. coli* would still respond to the one or more fragments (personal communication from S. H. Hutner). However, vitamin B_{12} is quite stable to dry heat. Macek and Feller (1955) found only a slight loss on heating at 120° C for 30 min. Shenoy and Ramasarma (1955) reported that the stability of the vitamin to prolonged heating depends on the inorganic milieu. They showed that iron gave excellent protection to the B_{12} activity of liver extracts when heated at pH 10.0 at 120° C for 30 min.

To date, it is not possible to obtain absolute values of vitamin B_{12} by available assay procedures. The *Ochromonas* and animal assays come closest, particularly after digestion by papain (Ford and Hutner 1955). Thus, it is likely that the values of vitamin B_{12} cited in this paper represent minimum levels. However, the procedures used were uniform and the levels of vitamin B_{12} do represent significant trends in its distribtuion. It would be desirable to make separate comparative studies of extraction and concentration procedures and to use different assay organisms in order to approximate more closely the absolute levels of vitamin B_{12} in detritus.

RESULTS

As described in the preceding section, samples of surface water were obtained at stations extending from the open ocean into a dead tidal river. The detritus level (mg/1) of each sample is shown in Figure 4 (solid line). It was observed that the detritus load increased progres-

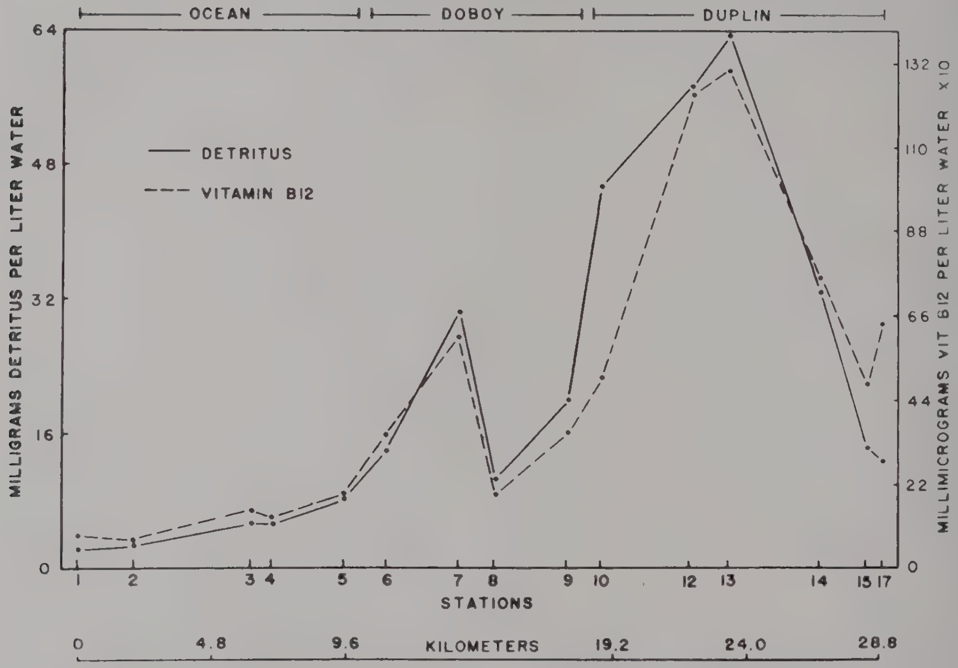

FIG. 4. Detritus load (mg/l) of samples 1-17 and the vitamin B_{12} content (mμg/l) of the detritus.

sively from comparatively low values at station 1 to a peak at station 7. During the time interval of collection, the tide was flooding (Fig. 2) and the waters at stations 6 and 7 were quite turbulent. Tide rips and eddy currents were observed at these stations. The decrease of the detritus content of the water sample from station 8 was attributed to settling-out at slack high-water as tidal velocities approached a minimum. From stations 9-13, progressive increases in detritus loads were encountered as the tide started to ebb and mixing of the sediments occurred. In addition the water at station 11 which was located at the mouth of a tributary entering the Duplin River (not plotted, see Fig. 1 for location) was muddy and turbulent. From stations 14-17, there was a progressive decrease in the detritus content of the water as the north end of the river was approached. Station 16 was not included in Figure 4 as it represented a situation similar to that found at station 17.

Also plotted in Figure 4 is a curve which represented the vitamin B_{12} content (mμg/1) of the detritus samples. On a basis of weight of the vitamin B_{12} per volume of water, comparison of the two curves indicated that the vitamin content though closely correlated with the weight of the detritus made up a somewhat variable proportion of it. The ratios of detritus levels to the amount of vitamin can be estimated from the vertical distances between each curve. In those cases where the vitamin curve is above the detritus curve, the ratio of vitamin to detritus is comparatively higher than in those cases in which the opposite situation is true.

In Figure 5 the vitamin B_{12} curve which is plotted on the basis of the weight of vitamin per weight of detritus is shown for comparison with the same detritus curve shown in Figure 4. These plots indicated that the relatively low detritus loads from the ocean samples were richer in vitamin B_{12} than the detritus from the turbid waters of Doboy Sound and part of the Duplin River. However, the headwaters of the Duplin River had relatively low detritus loads but contained the highest levels of vitamin.

In another series of experiments, samples of water (A-L) were collected at station 17 (Fig. 1) at time intervals over the course of a tidal cycle. The results are plotted in Figure 3. The tide curve is shown for comparison to the detritus load of the water and to the vitamin content of the detritus. The amount of detritus (mg/1) in samples A-C increased gradually up to the period of slack high water. During the interval of slack water, a sharp decrease was measured in water

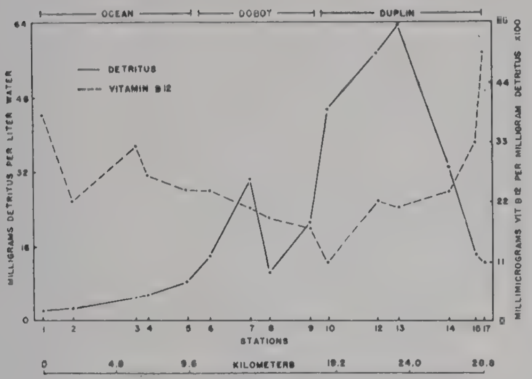

FIG. 5. Detritus load (mg/1) of samples 1-17 and the vitamin B_{12} content (mμg/mg) of the detritus.

sample D. This occurrence was followed by a gradual and steady increase in the detritus load of the water samples as the tide started to ebb (Samples E-J), and a gradual decrease at slack low water and the period immediately after low water (Samples K-L).

The vitamin B_{12} levels per weight of detritus and the detritus load of each sample are shown in Figure 3. During the flood tide, the waters became more turbid but the suspended matter contained proportionally less vitamin. Immediately before slack high water the detritus flowing into the marsh was poor in vitamin. In contrast, immediately after slack high water the detritus flowing out of the marsh was rich in vitamin. During the ebb tide, although the waters became more turbid, the vitamin values of the detritus decreased. From a point during the middle of the ebb tide to slack water, the vitamin content of the detritus leveled off. As the tide started to flood, the vitamin-rich detritus again became apparent as the bottom sediments were disturbed.

The bottom sediments were studied in another series of experiments. Mud samples were collected along the length of the Duplin River, and other samples were obtained from station 18 (Fig. 1) which was relatively sandy and devoid of marsh. The Duplin River muds contained an average of 0.13 mμg of vitamin B_{12} per mg, whereas the muds from station 18 contained an average of 0.007 mμg of vitamin per mg. A range of 0.01 to 0.50 mμg of vitamin B_{12} per mg of detritus was found throughout the experiments cited.

DISCUSSION

As a result of tidal action, the rich salt marshes of the estuarine environment in the vicinity of Sapelo Island are periodically flooded and drained. Throughout this flushing process, a continual exchange of nutrients occurs between the ocean waters and the marsh lands. Such an exchange of food substances could involve either the depletion or enrichment of one or the other source or serve the mutual advantage of both. The ecological effects of this process are readily noted by comparison of the numbers of plant and animal communities which inhabit a marshy coastal area and a sandy beach. In general the marshy area supports varied populations, whereas the sandy region is relatively unproductive insofar as different forms are concerned.

The essential nature of vitamin B_{12} for the growth and development of many microorganisms and animals is well established and has often been discussed. An attempt has been made in this investigation to follow the distribution of this growth factor found in detritus samples which were harvested from oceanic and estuarine environments. Samples of water were collected during the tidal cycle in order to compare the nature of the waters before and after flooding the marsh lands.

The relatively clear ocean waters contained detritus richer in vitamin B_{12} (average, 0.28 mμg/mg) than the more turbid sound waters and river waters (average, 0.21 mμg/mg). Significantly, the head waters of the river which meander through the marsh lands contained detritus richest in vitamin B_{12} (average, 0.47 mμg/mg).

Other experiments indicated that the waters entering the marsh immediately before slack high water contained detritus decidedly lower in vitamin B_{12} (average, 0.02 mμg/mg) than the waters which drained directly from the marsh after slack high water (average, 0.40 mμg/mg). When the vitamin-rich detritus did reappear as the tide turned and started to ebb, the marsh was still almost completely covered by water. On two occasions representing a time lapse of 42 days, samples were collected at station 17. These samples, 17 and D, were obtained 30 to 40 min after high water. In each instance, high tide was approximately 280 cm and the waters almost covered the tall *Spartina*. The levels of vitamin B_{12} per mg of detritus were 0.50 and 0.40 mμg respectively, whereas the average of 11 samples obtained during intervals of the tidal cycle was 0.10 mμg.

In addition, muds and sediments which were collected along the length of the river contained an average of 0.13 mμg of vitamin per mg of detritus. However, samples collected in a region devoid of marsh contained approximately 0.007 mμg of vitamin per mg of detritus. Both of these values were low compared to the maximum of 0.50 mμg/mg found in the waters which drained from the marsh immediately after slack high water. The mixing of the muds and sediments due to tidal action thus did not add appreciable quantities of vitamin-rich detritus to the waters.

Further study of the cycle of production and utilization of vitamin B_{12} in estuarine environments is necessary. Vitamin B_{12} is produced as a result of the activities of microorganisms and is utilized by both microorganisms and higher forms of life. It is possible that there is a more rapid production than utilization of vitamin B_{12} in the marsh, and a more rapid utilization than production in the muds and sediments.

SUMMARY

Microbiological assay procedures were used to measure the vitamin B_{12} content of detritus which was harvested from water samples by filtration. Surface water was collected at stations ranging from the open ocean, through a sound, and into a tidal river. On the basis of weight of vitamin B_{12} per weight of detritus, comparatively high values of the vitamin were measured in the detritus from offshore waters. The smallest amounts were found in the detritus of the sound waters. Significantly, the highest values of vitamin B_{12} were obtained from samples collected near the head-waters of the river which meander through rich *Spartina* marsh. Subsequent experiments were performed over the course of a tidal cycle at one station located near the head of the river. The waters which drained from the marsh immediately after slack high water contained detritus richer in vitamin B_{12} than that found in samples which were obtained immediately before slack high water and during the ebb tide to low water. Values of vitamin B_{12} per mg of detritus obtained by our procedure ranged from 0.01 to 0.50 mμg; this is considered a minimum value for technical reasons.

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USES OF MARKING ANIMALS IN ECOLOGICAL STUDIES: INTRODUCTION[1]

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Study of plants and animals is designed primarily to obtain information about their operation under natural conditions. They may be taken into the laboratory or museum for studies that can be made under abnormal conditions. Morphological studies of bodies, skins or shells may yield valuable information, but studies of physiology or behavior of organisms held under abnormal ecological conditions may be misleading.

The ease with which laboratory and museum work can be conducted has in the past led to underemphasis of field work which in general, is so much more difficult to perform. There is now developing a trend in the direction of checking results of laboratory and museum work against normal operations in nature.

This is more difficult that it seems because of the difficulty of controlling or evaluating the dynamic flux of many factors that are continually at work affecting their well-being. And yet, this is the thing that gives field work so much importance. Where ecological factors cannot be adequately controlled in nature, certain aspects of the problems may be tested in the laboratory, but the results must be taken back to the field for proper evaluation.

For example, the taxonomy of species and subspecies derived from the study of morphological characters of innumerable specimens in museums must be continually revised in light of intraspecific studies made in the field. In areas where knowledge of ecological conditions is essential, planned collections in critical areas may help to solve problems of intergradation, hybridization or overlap. A few years ago, in recognition of the need to supplement the immense laboratory program with back-to-nature studies, an organization was formed for "The Study of Animal Societies under Natural Conditions."

In studying animals in the field it must always be kept in mind that movements, behavior patposes, if in addition to place or locality, needed for plotting geographical distribution, the ecological habitat, community or niche be also recorded on the tag with the specimen. This will allow plotting of the ecological distribution, which in many cases is as vital as geographic distribution. To be effective, however, this requires a stable ecological taxonomy that everyone can use. (Woodbury, Science, **115**: 3, 1952.)

In studying animals in the field it must always be kept in mind that movements, behavior patterns, and social relationships are difficult to study. One of the most critical and difficult problems in such studies is the recognition of animals to be studied. From the far distant past down to the present time, the difficulty of recognizing individual animals time after time has haunted natural history and ecological studies with shadows of doubt. It required close personal acquaintance with individual animals to provide certainty of recognition until the idea of placing artificial marks on animals was developed. Since then, many schemes of marking animals for individual identification have been devised. It is the problem of this symposium to analyze these methods and trace the results that have flowed therefrom.

The papers will follow in sequence.

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[1] Symposium given at an Ecological Society session of the A A A S meetings at Berkeley, California, December 27, 1954.

USES OF MARKING ANIMALS IN ECOLOGICAL STUDIES: THE MARKING OF FISH

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INTRODUCTION

The origins of fish marking and tagging go back to a dim past, but the first carefully planned and successful tagging was done by C. G. Atkins on Maine salmon in 1873, according to Rounsefell and Kask (1945). For two decades afterward, tagging was principally a salmon-fisherman's hobby. Limited numbers of tags made of materials like silver and platinum were used. Marking of utilitarian fishes on a large scale began in Denmark in the 1890's; C. G. J. Petersen affixed tags to plaice and also punched holes in their fins.

Both tagging and mutilation have been widely used and have proved to be powerful tools for studying population ecology.

The qualifications of a perfect tag or mark would include the following:

(1) It should not affect the mortality rate or the behaviour of the fish, either immediately or cumulatively.

(2) It should make the fish neither more nor less liable to be captured by fishing gear, than are unmarked fish.

(3) It should identify the individual fish.

(4) It should be retained by the fish indefinitely and should be readily observed by those from whom recoveries are expected. (Also, it should preferably pass unnoticed by those from whom recoveries are *not* desired: in some types of experiment only recoveries made by special observers are of value, and prior removal of some tags by others is disturbing.)

Obviously it will rarely be possible to obtain a perfect tag or mark, meeting all the above requirements. For many purposes one or more of them are unnecessary, or can be relaxed with little loss of information. Good design in marking experiments consists of choosing the tag or mark most appropriate for the end in view and for the means of recovery available, and then in making certain that the recovery procedure does in fact operate efficiently.

Marking by Mutilation

By far the most popular mark for fishes has been the removal of one or more fins—wholly or in part. Though this procedure does not permit recognition of individual fish, except in small-scale experiments, it is often accomplished with less injury to the fish than tagging involves, and can be used on smaller individuals. For short experiments, instead of removing a whole fin only a part of it may be cut off, or a hole may be punched in it.

Before starting a marking experiment, it is usually desirable first to sample the population for natural incidence of the mutilation proposed. In salmonids, for example, this incidence is sometimes high enough to be disturbing when single fins or both fins of a pair are used, *and* when only a small fraction of the total stock will be marked. If two unrelated fins are used, or if a fairly large fraction of the stock (say 1 percent or more) has been marked, natural mutilations are relatively so scarce as to be of little significance.

Regeneration must be tested in each experiment separately. In general, regeneration seems to be more common or more complete among spiny-rayed fishes than among soft-rayed fishes, among small fish as compared with large fish, and in warmer as compared with cooler waters. Also, median fins tend to regenerate more quickly and perfectly than paired fins, and the closer a fin is cut, the less the likelihood of regeneration.

Quantitative recovery of fin-clipped fish must be done by specially assigned observers, and it is desirable to have enough fish marked so that they are encountered frequently (at least one in 1000); otherwise attention of the observers tends to flag.

Tagging

Rounsefell and Kask (1945) have described and illustrated the kinds of tags used up to the early 1940's. Some of the more successful types are as follows:

1. The popular Petersen discs: two baffles attached by a wire or filament through the fish's body, gill cover, or fin.
2. Cattle-type strap tags and similar bands or rings, clamped around the mandible, maxilla, or operculum. Relatively few fish retain these types of tag for long periods, and some shed them very quickly. However opercular straps on halibut, and rings around the maxillary of lingcod, have been recovered after many years (Thompson and Herrington 1930; Hart 1943a).
3. Streamer-type tags, usually attached by wire or nylon through the body or fin base, and with a metal disc or a "hydrostatic" cylinder trailing behind. For short experiments with very small fish, simple colored threads strung through the base of the dorsal fin have proved useful.
4. Internal tags, put into the body cavity: these are made of bright-colored plastic for recovery by hand, or of metal if recovery is to be by magnet or induction detector. There have also been recent trials with radioactive cobalt internal tags.
5. Recently in California, hollow plastic tubes have been threaded through the bodies of ocean fishes (Wilson, 1953). They have given the first satisfactory recoveries from Pacific tunas and work well with some other fishes.

In choosing a tag, the most important consideration is whether or not the fish can be individually inspected for recoveries. If not, mechanical recovery by magnet, induction coil or radiation counter is necessary. In general, this has proved more expensive and less satisfactory than individual recovery—so much so, that in a borderline case it might be desirable to inspect individually a rather small fraction of the catch and increase the number of tags put out as much as feasible. The fraction of the catch inspected should of course be a known one, and so far as possible a random one.

Where untrained observers must make the recaptures, a conspicuous tag is indicated. Return of tags can be encouraged by publicity, by frequent visits from a collector, and by cash rewards. In this way very substantial percentages of strap tags or Petersen tags, for example, have often been returned. To check on the efficiency of this type of recovery it is desirable that *a portion* of the catch be inspected by trained personnel, if this is at all feasible.

Most difficult of all to assess, usually, are the rate of loss of tags from the fish, and the effects of tagging or marking upon the mortality rate and catchability of the fish. However, much ingenuity has been used in getting information on these matters, even with so difficult a subject as the wide-ranging California sardine or pilchard (Clark and Janssen 1945; Janssen and Aplin 1945). Sometimes apparently minor changes in procedure make for important improvements in recovery rate. For example, the tightness with which strap or Petersen tags are affixed can seriously affect their staying power, snug attachment being unfavourable (Hart 1943a; Manzer 1952).

Holding fish in enclosures will often shed light on immediate mortality or tag loss, but it is less useful as a quantitative index of sustained mortality or loss. In removing fins from small fish, the immediate mortality from shock may be quite small but the permanent handicap of a missing fin in a dangerous environment may add up to a serious increase in mortality rate. With larger fish the immediate mortality is more likely to be important, particularly with species that are brought up from considerable depths or which injure themselves in the gear. However, with a suitable technique for tagging, in certain species, a high degree of success has sometimes been achieved with little or no mortality of either sort.

Both in tagging and in marking, the use of sedatives like urethane or sodium amytal can sometimes speed up the process and reduce injury or discomfort to the fish.

Movements and Migrations

One reason for marking or tagging fishes is to learn about their movements. Examples of movement over long distances always attract attention; some of the more striking ones are shown in Figures 1 and 2.

The various species of tuna are at home in pelagic waters of the warmer oceans. They have long been suspected of much traveling, and movements of bluefin tuna between the Mediterranean and the Atlantic were early recognized by means of hooks accidentally retained by and recovered from the fish. However few would have predicted the frequent transpacific crossings which are now suggested by preliminary results with albacore. Two have moved from California to beyond Midway Island, and one went 5300 miles to a point 550 miles SE of Tokyo in 10 months. (Blunt 1954; Ganssle and Clemens 1953.)

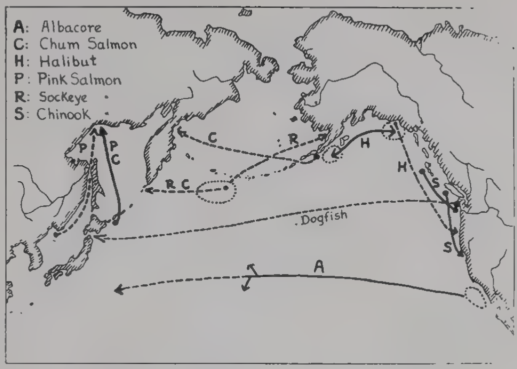

FIG. 1. North Pacific Ocean, showing fish movements as determined by tagging. Solid lines indicate frequent movements, dotted lines infrequent movements or those for which there is little information as yet. The lines do not necessarily indicate the paths followed by the fish. (After various authors.)

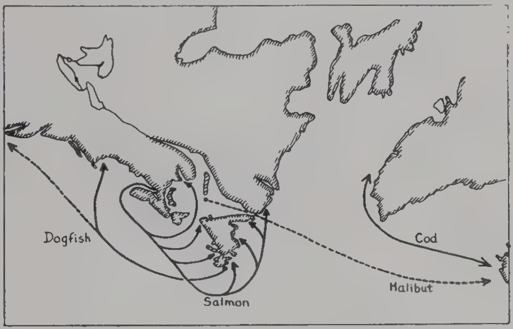

FIG. 2. "Side view" of the northwestern part of the Atlantic Ocean, showing frequent and infrequent movements of fish, as indicated by tagging or marking. The marked salmon shown came from the Petitcodiac River in the Bay of Fundy; there was also a similar distribution of smolts marked on the Miramichi. (After various authors.)

Though movements of tuna over thousands of miles were not unexpected, it came as a shock to learn that the homely shore-frequenting dogfish also is a great traveller. One individual was tagged at Willapa Harbour, Washington, and after 7½ years turned up in Tsugaru Strait, Japan (Kauffman 1955). The most direct distance is about 4400 miles, but the dogfish is likely to have stayed fairly close to shore, so his total journey was probably at least as great as the albacore's. Other Pacific dogfish moved considerable distances along the American coast and, in the Atlantic, several went from St. John's Newfoundland, south to Massachusetts and even Virginia (Templeman 1954).

Though the above species are exceptional, many marine commercial fishes swim long distances. For example tagged Pacific halibut, though most frequently retaken within 100 miles of the point of tagging, apparently make fairly regular journeys across the south coast of Alaska, and a few individuals moved from that region down to the latitude of Washington or Oregon (Thompson and Herrington 1930). Similarly, halibut tagged in the Gulf of St. Lawrence nearly all were recaptured there, but one individual got as far as Iceland (McCracken, 1955).

For fishery management, the *typical* migration pattern rather than the exceptional event is of most interest. Metal tags recovered in reduction plants on the coast of British Columbia, during the 1940's, proved that the local body of California northern offshoot of the main body of California fish, which typically returned south each winter (Hart 1943b). The herring, by contrast, not only comprise a native population, but a number of rather distinct local populations have been distinguished and are regulated separately (Hart, Tester and Broughton 1942). In this case the populations had mostly already been distinguished by average differences in meristic characters; the tagging supplemented this picture and indicated the amount of interchange between populations.

The most striking demonstrations of individuality of populations have been with the various salmons. Clipping fins from a portion of the sockeye salmon smolts leaving Cultus Lake, British Columbia, had indicated a large number of returns to that spot. However the marked ones were found to be only two-fifths as numerous, proportionately, as the unmarked, suggesting the possibility of extensive "straying." Fortunately it was possible to mark *all* the smolts in two later years, and the returns from those years showed less than 1 percent straying (Foerster 1936). The poorer percentage of returns of marked individuals was evidently the result of a serious marking handicap.

Even when there is no chance of marking *all* smolts in an area, discreteness of populations can be proven somewhat indirectly. Figure 2 shows diagramatically how this was done for several Atlantic salmon stocks (Kerswill 1955). Marking of smolts in the Petitcodiac River and two branches of the Miramichi, in New Brunswick, yielded large numbers of returns in the commercial fisheries, particularly off Newfoundland. At the same time the marked fish returned abundantly to their home streams, but none at all were taken in the several Newfoundland streams examined. Nor were they seen in other New Brunswick or Quebec streams where search was made. Thus it was possible to obtain proof of substantially complete segregation of various river races, and their regular return from long distances—an often-disputed thesis, which nevertheless must be the cornerstone of Atlantic salmon management.

The whereabouts of Atlantic salmon during their sea life, before the spawning migration, has not yet been determined. In the Pacific, chinook and coho salmon can be caught just offshore, and tagging experiments during the 1920's indicated extensive movements down the coast (Clemens *et al.* 1939). The more abundant but more elusive pink, chum and sockeye salmon have not yet been followed in their journeys away from and back to the American coast. However, from the Asiatic side they were followed far out to sea during the 1930's by Japanese pelagic gill-netters, who have done a certain amount of tagging (Anon, 1955: see also Fig. 1).

Preliminary results suggest an area of mixture of Alaskan and Siberian stocks in the region of the western Aleutian Islands. To define more accurately the extent and importance of such mixture is one of the principal concerns of the recently organized International North Pacific Fisheries Commission. Brief mention must be made of the use of tags in fresh water to identify times and speed of migration, and reaction to obstacles. Some of the problems and results of this kind of work are given in papers by Thompson (1945), Ricker (1947), Talbot (1950) and Godfrey *et al.* (1954).

Movements of non-anadromous fishes in fresh waters studied by Scott (1949) and Gerking (1953) have demonstrated that marked river fishes mostly stay in or return to the same "holes" for years at a time, being dislodged neither by spring freshets nor by the muddy torrents which follow summer cloudbursts. This is the more interesting because fyke-netting on the flood plain during high water showed that at least some of these fish did move out of the normal channel and fed on the abundant earthworms. Fishes brought in to a stream from outside are apparently much less likely to remain where they are put, though a well-controlled comparison has not yet been made. Trout displaced from their original homes in a small river tended to move back to them (Miller

1954). In lakes, similarly, release of tagged fish where they were caught has often been followed by recaptures predominantly in the same place: an early example is an experiment on pike by McKenzie (1930). Also, when fishes in a small lake are marked and moved to a part of it other than their "home," most species show considerable ability and inclination to return to the original site (Ball 1947; Shoemaker 1952).

GROWTH, SURVIVAL, EXPLOITATION AND ABUNDANCE

For most fishes the most important use of tagging and marking has been to help estimate the vital statistics, or biological statistics, of their populations. Treatments of suitable methods and computations have been given by Ricker (1948) and by Rounsefell and Everhart (1953).

Growth. Growth of fishes is estimated mainly from marks on scales, otoliths or bones. However, the observed growth of tagged fish after a year or more of freedom can provide a check on accuracy of other methods, particularly for larger fish where ages from scales or otoliths tend to be uncertain. Because some kinds of tags have been found to slow up the fish's growth, the method must be used cautiously.

Survival rate (s). When rate of fishing is constant from year to year, recaptures (R) of marked individuals in successive years are used directly to estimate survival rate; i.e., $s = R_2/R_1$. Such an estimate is not affected by any temporary hardships of the tagging or marking procedure, provided some interval is allowed for recuperation before the first year's recoveries begin. If rate of fishing varies from year to year, this can be taken into account for survival estimates. Possible procedures are to mark fish in two successive years, or to use information on the level of fishing effort which prevailed (formulae 39 and 38 of Ricker, 1948).

Survival estimates obtained as above are usually used to check estimates made from the age distribution of the population. Most of the potential sources of error are different in the two methods so that, when they agree, the result can be treated with considerable confidence.

Rate of exploitation (u), *and population* (N). The fraction of fish removed from a population by a fishery is the basic datum for all management procedure. Usually only marking experiments can supply it directly. The simplest situations are very simple indeed: a representative body of fish (M) is marked just before the fishing season, and that year's recaptures (R) are tabulated, so that $\hat{u} = R/M$. Further, if total catch (C) is known, the vulnerable population of fish is estimated as $N = C/\hat{u} = CM/R$. This last is commonly called the Petersen formula, and it will probably long be used; however maximum likelihood has indicated an alternative form, $N = M(C+1)/(R+1)$, which is appreciably more efficient when recoveries are few (Bailey 1951).

Unfortunately few real experiments are this easy. Often it is impossible to mark fish quickly just before a fishing season, and in that event their natural mortality prior to fishing must be accounted for. If marking and recovery both extend through the fishing season, the Petersen method must be elaborated into a "Schnabel" or other similar estimate. For a variety of reasons there may be unrepresentative recoveries—either too many or two few—during the first few days, weeks or months of an experiment. For example, Chatwin (1953) describes serious potential sources of error in what seemed at first sight to be a straightforward piece of work. An important and often ignored complication in long-term experiments is a change in vulnerability of the fish as they grow older; or the vulnerability of all fish may vary from year to year. Most of the varied procedures which have been proposed to adjust for the above systematic biases are discussed in one or both of the general works cited at the beginning of this section.

A different method of treating a large-scale marked fish experiment is to relate the recoveries per unit of fishing effort to cumulative catch throughout the fishing season, and from that to compute survival, catchability and rate of exploitation. DeLury (1951) proposed this as a modification of the Leslie method (which does the same thing with unmarked individuals) mainly in order to check the assumptions on which the latter depends. Under favorable circumstances, however, differential response of the marked and the unmarked can be interpreted in terms of emigration from and immigration into the stock, and can be used to estimate these effects quantitatively (Ketchen 1953).

SUMMARY

Since the 1870's, fish have been marked by affixing tags and by removing fins. Recaptures are used to indicate movements and migrations, discreteness of populations, rate of growth, overall mortality and survival rate, rate of exploitation by a fishery, natural mortality rate (by difference), and actual population size. Quantitative information from marking is rendered uncertain by possible systematic biases of varied types. However, reliable results have sometimes been achieved by

careful selection of the most suitable tag or mark, combined with a recovery program of tested efficiency.

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USES OF MARKING ANIMALS IN ECOLOGICAL STUDIES: MARKING AMPHIBIANS AND REPTILES

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The marking of amphibians and reptiles for individual identification developed during the third and fourth decades of this century and soon became popular among herpetologists.

MARKING AMPHIBIANS

As early as 1921, McAtee (1921: 39) studied homing tendencies in bullfrogs by moving a tame frog with a missing front foot from its home range and watching for its return. Breder, Breder and Redmond (1927: 201-229) tied numbered tags around the waist of frogs and obtained accurate data about specific activities and behavior.

By 1931, it was recognized that the practice of assigning ages to frogs on the basis of size classes needed experimental support. Wright (1931: 59);

in his studies of the Okefinokee Swamp suggested that "what the resident naturalist can do is to mark frogs or keep them in some pond enclosure and get the real growth of an individual or individuals."

This suggestion was used by Hamilton (1934: 88) in studying the rate of growth of the American toad near Ithaca, New York. He marked the toads by incising one or more toes of the fore feet but he did not describe his system of records. He was, however, able to measure and weigh specific individuals from time to time and get accurate information on their growth rates.

In 1939, Raney (1940: 733-745) marked over 600 frogs and toads by the jaw-tagging method in Albany County, New York, and was able to obtain specific data on movements of individual animals which yielded pertinent information about the sex ratios, behavior patterns of reproduction, daily and seasonal movements and other natural history information. He concluded that the jaw-tag method of marking frogs was entirely satisfactory and superior to such other methods as incising toes or attaching a numbered tag around the waist. He felt that the bookkeeping was too complex in the toe-clipping method and the waist-tied tag was too impermanent. His jaw-tagging method was an adaptation from the fish jaw-tagging method reported by Shetter (1936: 651-653) in Michigan.

Experiments with tagging small salamanders were later reported by Raney (1941: 578). He did not find any commercial jaw tags suitable for such small animals and his experiments of attaching small clips to back or tail muscles of salamanders proved unsuccessful.

Despite Raney's objection to the complex bookkeeping involved with the toe-clipping method, Bogert (1947: 5) used the method in absence of suitable tags and was able to obtain 250 combinations by clipping only one toe per foot, by means of which he was able to study homing problems.

In a study of the narrow-mouthed toad (Microhyla), Freiberg (1951: 374) clipped toes, through the joints nearest the base with fine scissors. He found little tissue regeneration during one year's observations.

A method of toe-clipping and a comprehensive method of bookkeeping with a capacity of 6399 individuals was reported by Martof (1953: 165-174), in which the toes were designated, beginning at the outside, 1 to 5 on the left hind foot; 10, 20, 30, 40 and 50 on the right hind foot; 100, 200, 300 and 400 on the left front foot; and 800, 1600, 2400 and 3200 on the right front foot. He felt that he had overcome Raney's objections of complicated bookkeeping and that this was a satisfactory method of marking frogs.

A further modification in the toe-clipping method was used by Carpenter (1954: 197-200) in which he designated the toes by letters and gave numbers to individuals corresponding to combinations of the letters, thus the front toes beginning at the outer left were designated A to H and the hind toes (stretched backward) in the same order I to R. Numbers were given to combinations of letters, viz. 1-AB, 2-AC, 3-AD, 10-AK, 17-AR, 18-BC, 25-BJ, 33-BQ, 34-CD, etc. The first time the animal toe-clipped AK was captured, it would be recorded as 10(a), the fifth time 10(e), etc. A further possibility of modification would be to record only the letter combinations in alphabetical sequence and add the sex sign, thus AK ♂ or CD ♀ and recaptured 4th time CD ♀ (4).

Studying salamanders in California, Stebbins (letter Nov. 17, 1954) decided to concentrate upon toe-clipping after many experiments with other methods. He and his students did not find the use of dyes or jaw tags satisfactory for individual recognition. The jaw tags caused considerable irritation and were often sloughed off through the jawbone and lost.

One of his students (Hendrickson, 1954: 6) reported unsatisfactory results with tattooing and with clipping skin from costal folds. Tattoo marks spread through sub-dermal spaces and were not permanent. Clipping the costal skin folds was injurious to the animal and the resulting scar often was not permanent. Toe-clipping, the most practical method, was handicapped by regeneration of toes, but the process was slow and regenerated toes could usually be recognized.

Marking Reptiles

Among lizards, as among frogs and toads, toes clipped in various combinations provide an easy and useful method of identification used by many people. The same systems used on amphibians will apply to lizards.

By clipping 1, 2, 3 or 4 toes on different feet in different combinations, several hundred lizards could be individually identified. It is convenient to letter the feet, number the toes and give the sex in designating lizards, thus A2D3 ♀ indicates that the second toe of left front foot and the third toe of the right hind foot of a female were clipped. It is conceivable that toe clipping might be deleterious to the safety of lizards but apparently specimens survive without much indication of harm.

Among snakes, which have no toes to clip, two principal methods of marking are scale clipping

(Blanchard and Finster 1933) and tattooing (Woodbury 1948: 127-128, 1951: 5-7). The method of scale clipping used by Blanchard in Michigan and others is a simple method which can be used in the field with very little difficulty. For equipment, this method requires only a pair of small scissors which can be carried easily on the person. Ends of the ventral plates are clipped in various combinations. Certain precautions are necessary for accuracy. At least one case (Conant 1948 has been reported in which the clipped scales regenerated in 4 or 5 years, thus throwing doubt upon its reliability.

Ordinarily the anal plate in front of the transverse vent is used as the point of reference. Counting forward from that point and clipping either the right or left ends of the ventral plates, gives opportunity for several hundred or even thousands of different combinations that will give individual identification. A convenient way of indicating the points clipped is to represent plates running forward from the anal plate by letters of the alphabet, using a capital letter for the end of the plate on the snake's right side and a small letter for the other end.

Thus, if the fourth plate is clipped on a female snake's right side, and the seventh on the snake's left side, it would be designated as Dg ♀. Similarly a designation of Bek ♂ would indicate a clipping of the second scale on a male snake's right side and of the fifth and eleventh scales on the snake's left side. In this method, there is the ever-present danger of miscounting plates or mistaking right or left ends of plates either in making the original records or in identification when recaptured.

The other method consists in tatooing individual numbers on snakes. This requires a portable battery-operated tattoo outfit suitable for field work. The power must be sufficient to drive the tatooing needles through the scales and leave ink underneath. Numbers may be written on any smooth light colored surface where colored pigments do not obscure the ink, such as the throat region or the base of the tail.

In this method, there is the ever-present danger of misreading the numbers when recaptured. For this reason great caution should be exercised in making the figures when tatooing at the time of the first capture. The free ends of such figures as 2, 3, 4, 5, 6 and 9 should be made extra long to aid in distinguishing from each and from figure 8 without any free ends. If once properly tattooed so there can be no mistake in reading, the number will serve as a permanent identification of adults. Neither method handicaps the snake after recovery from the operation of marking.

Turtles with their their hard shells offer other methods of marking. They are difficult to tattoo although the method has been tried on soft parts. Toe clipping has been used but seems best suited as an auxiliary to methods of marking the shell. Shell marking offers promise of greatest usefulness. Painting, carving, branding and grinding edges are methods that have been tried.

Painting the carapace of land tortoises has been used by many amateur naturalists. Woodbury and Hardy (1948: 149-150) painted various combinations of plates using various combinations of colors for individual identification but found that the colors began to wear thin after a year or two and discarded the method in favor of branding. However, one red painted tortoise that did not get branded was definitely identified by means of the paint more than 8 years later.

Branding tortoises with a wire heated in a small fire proved to be a practicable way of marking that was more or less permanent if properly done. There are, however, some dangers inherent in the method and some precautions to be taken. If the burning of the shell goes too deep and affects the underlying tissue, it initiates a slow process of regeneration which after a few years completely replaces the burned area and obliterates the brand. This can be avoided by using a white-hot wire of about 12 or 14 size and burning the shell so quickly that the heat does not damage the underlying living cells.

In practice it is convenient to put a brand on various plates or combination of plates. A convenient method of recording the combinations used is to designate the vertebral plates by capital letters, A to F, the costals by numbers 1 to 8 and the marginals by small letters a to v. An individual can then be cited by giving the combination of plates branded followed by the sex symbol, thus De ♂, B6 ♀, A5r ♂, 5g ♂, ev ♂.

John T. Nichols of the American Museum marked box turtles for many years (1939: 14). He used a method of carving numbers on plates and found that the numbers were distinct after 10 or 15 years on turtles that did not molt the outer plates. On tough-shelled turtles, this would be a slow and difficult procedure if carved by hand.

A method of marking turtles by making notches in the edge of the marginals was developed by Fred R. Cagle (Copeia, 1939: 170), in which scissors and files were used but later (Mus. Zool., Univ. Mich., 1944: 7) a power grinder where electricity was available was suggested as much more efficient in making the notches. As a substitute for this last item, a small portable hand grinder might be carried in the field where there is no available source of power.

Cagle reported that notches could be cut with scissors on small unossified shells. Hard shells had to be sawed or filed, but when such notches were once established, they appeared to be permanent identification marks that did not interfere with normal activity of the turtles.

He suggested numbering the marginals separately on each side beginning with the plates next to the nuchals, but probably an improvement would result from lettering the plates as suggested for snake clipping, using capital letters on one side and small letters on the other. He calculated that 16 turtles could be marked by making a notch on only one plate, 120 by using two plates on each, 560 by using three and 1820 by using four, a total of 2516 possibilities.

The previous methods of marking have been designed for permanence but for studies of molting, sometimes auxiliary marks are useful. Fitch (1940: 152) reported marking lizards externally with indelible ink which was shed at the next molt. Those that retained the ink until subsequent capture were known not to have molted, but those that had lost it were known to have molted at least once.

In the author's work with a snake den in Tooele County, Utah, a method was developed of marking rattles on rattlesnakes with a cuticle or keratin-staining carmine dye which was useful in determining the number of rattles added and consequently the number of molts that had occurred since the staining was done. This helped greatly in adding certainty to the method of determining ages of rattlesnakes (Woodbury *et al.* 1951: 28-40).

CAPTURING ANIMALS

Marking reptiles for individual identification generally requires capture of the specimens so they may be marked and processed to get data desired Capturing reptiles by hand is generally a tedious and time consuming process and hence has led to the development of more efficient methods by the use of special techniques, tools and traps. Many ingenious devices have been suggested.

For capturing small lizards that hide in bushes, cautious and careful slow movements are essential. A pair of long forceps or a stick from a native bush can be pushed slowly toward the lizard and pin down a foot. For those out in the open, a toy rubber throwing-gun or sling-shot full of coarse sand or fine gravel may sometimes stun a lizard so that it can be picked up, but ordinarily a large percentage of such cases prove detrimental or fatal.

Probably the most useful methods are trapping. Wm. Vogt (1941: 115) suggested a lizard trap consisting of a flat box about 1 meter square and 5 centimeters (2 inches) high with a screen bottom, a screen funnel opening in one corner and a door in the opposite corner. To empty the trap, turn it over and open the door into some dark container into which the lizards can run. Set the trap in the open, in an area where lizards occur. Acting as a shelter, it entices the lizards through the funnel without bait.

R. H. Imler (1945) suggested a method of capturing snakes by setting funnel traps along a mesh wire fence. Snakes encountering the fence tend to follow it and enter the traps through the funnels. This method has been applied in various ways, notably in snake "pest control" in South Dakota (Gloyd 1947: 87), in population studies of snakes at Patuxent, Maryland (Dargan and Stickel 1949: 264), and in snake dens in Tooele County, Utah (Woodbury *et al.* 1951: 1); in Kansas, Fitch (1951: 77), used a modification of Imler's method—cylindrical traps with removable end funnels set in natural reptile pathways without the use of fences. Carpenter (1953: 183) used Fitch's type of modified cylindrical traps in shallow water along the shore of ponds for catching salamanders, frogs and other animals.

In Woodbury's snake den studies, a screen wire fence about 330 feet long was used to enclose a cobblestone rock area where hundreds of snakes went underground for winter and emerged in the spring to spread out over surrounding territory. Funnel traps opening outward through the fence in the spring and inward in the fall, captured the snakes coming and going.

TAKING DATA

The capture of amphibians and reptiles offers a golden opportunity to gather useful information about them while they are being processed. Measuring and weighing are common methods that yield information of increasing value with the increasing data. Flexible steel tapes graduated in millimeters and inch fractions in pocket sizes are handy for gross measurements, but calipers of different sizes with similar graduations are essential for more precise measurements or for direct measurements of length of a chord of arc around curved surfaces.

Routine measurements usually include body and total lengths as well as any other set of minor measurements desired for special study. With turtles, it is usually desirable to get measurements of length, width and depth of the shell and certain other special measurements.

The problem of weights is more difficult because of the difficulty of carrying suitable scales or balances in the field. Total weight taken at successive times yields information of value if due consideration is given to food intake, evaporation and excretion. Weights taken before and after hibernation when the food problem is not involved, show loss in weight during winter dormancy. Weights taken in spring and fall give data on growth during the summer season, but the best idea of growth in weight comes from comparison of weights either before or after successive hibernations.

In addition, valuable information can be obtained from reptiles by counting scales or other structures for special purposes or in some cases by palpation of certian lizards and snakes. By manipulating the thumb carefully over the abdomen of females, it is often possible to detect or even count large eggs in ovary or oviduct.

USES OF DATA

Accumulation of such information provides a foundation from which significant ideas can be derived, answering such questions as: How fast does the animal grow? Does it continue to grow all its life? What is the reproductive potential? How large is a home range? Does one home range overlap another or are they mutually exclusive territories? Are there any social attractions between them? and so on.

When such questions can be answered, field studies will yield results of significance.

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USES OF MARKING ANIMALS IN ECOLOGICAL STUDIES: MARKING BIRDS FOR SCIENTIFIC PURPOSES

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HISTORICAL RECORD

The migratory flights of birds between their summer and winter homes are among the most interesting of all natural phenomena and have intrigued man's imagination from the earliest dates of history.

More than 3,500 years ago the early writers of the Old Testament were well aware of the seasonal movements of birds (See Exodus 16: 13; Numbers 11: 31; Job 39: 76; Jeremiah 8: 7).

Recognition of bird migration is evident in the writings of Homer, Hesiod, Herodotus, and Anacreon long before the Christian Era (Lincoln 1939, 1950; Wetmore 1927.) Later Aristotle and Pliny the Elder wrote concerning it. Persians, Arabs, and other early peoples based part of their calendar on the data taken from bird movements. Some of the Plains Indians in America believed that the bluebird bore summer to them on its azure wings. Among certain Eskimo tribes, the period of late March and early April is referred to as "The coming of the birds."

Because of the universal interest in bird migration it is natural that bird banding should develop as a means of learning more about birds and their movements. The earliest scientific record (but one which has been questioned) seems to be that of a great gray heron (*Ardea cinerea*) captured in Germany in 1710, which carried on its tarsus several metal rings, one of which indicated that it had been placed on the bird in Turkey several years earlier (Wetmore 1927: 12-13; and Lincoln 1950: 108).

Audubon, about 1803, marked wild birds with silver wire to identify them. Folklore in Europe at still earlier times told of messages carried by storks between Europe and Africa. Lord Wm. Percy in England placed rings (bands) marked with the year of banding and the letter "N" on the tarsus of European woodcock between 1891 and 1908 (Lockley and Russell 1953). In 1899 C. C. Mortensen in Denmark was the first to start scientific banding. He used numbered aluminum bands and systematically banded storks, teal, starlings and other birds. Dr. Paul Bartsch in 1902 banded black-crowned night herons in Washington, D. C. and was the first to use numbered bands in America. Each band had the return address of the Smithsonian Institution of Washington, D. C. In 1905 J. H. Fleming of Toronto began bird banding in Canada with the use of numbered bands. In 1909 the American Bird Banding Association was organized largely under the leadership of Dr. L. J. Cole and P. A. Taverner. This stimulated and popularized bird banding. In 1909 Jack Miner commenced banding ducks and geese at his famous bird sanctuary at Kingsville, Ontario. On nearly all bands he hammered out a Bible quotation.

Bands of different kinds have been used to identify birds. However, the type applied most extensively is the aluminum leg band. This kind of marker will be implied in comments here except where other kinds of bands are specified. Colored non-metal bands for legs or neck and various other methods of marking or coloring have been used and will be discussed.

BIRD BANDING IN AMERICA

Since 1920 bird banding in the United States (including Alaska) and Canada has been done under Federal supervision and by permits from the respective governments. Records from these studies have been maintained by the U. S. Fish and Wildlife Service (until 1940 known as the Biological Survey). Canada maintains duplicate records of banding done in that country and also of return records obtained there.

Since the establishment of the Biological Survey in 1885 our Federal agency has been accumulating data on migration and other facts pertaining to birds. The records are now filed at the Patuxent Research Refuge, Laurel, Maryland. To coordinate, unify, and simplify the banding system, and to prevent duplication of effort, all banders of migratory birds in both countries (with the single exception of the banding at the Jack Miner Sanctuary, Kingsville, Ontario) follow the same general system of record-keeping and use the same type of bands which are stamped, "Notify U. S. Fish and Wildlife Service, Washington, D. C." By agreement, the Wildlife Branch of the Canadian Government is promptly furnished reports on return records of all birds banded in Canada. This coordinated North American agreement has a distinct advantage over the European program in which each country has a separate system of banding, numbering and record-keeping. To facilitate their work most bird banding organizations in various countries link themselves with each other by correspondence and exchange of records. Scientific bird banding is unique in that it needs and invites the aid and cooperation of interested and qualified private citizens.

Bird bands with the stamped or engraved serial number and return address are of light rust-proof metal, usually aluminum, and are made in different sizes to accommodate the legs of different kinds of birds. Monel metal and copper compound bands have been tried but found unsatisfactory. Techniques of banding and trapping are described in many bird books and magazines. A splendid manual for bird banders by Lincoln and Baldwin (1929) gives a succinct summary of methods known up to 1929. The Canadian Wildlife Service, Ottawa, sends to each Canadian bander an excellent 14-page processed paper giving details, procedure and policies applicable to bird banding in that country (Anon., n.d.).

Anyone finding a dead bird with a band or otherwise obtaining a used band should forward the band or the exact information contained on it to the U. S. Fish and Wildlife Service, Washington 25, D. C., along with all pertinent data including the date and place of collection, name of collector, identification, age and sex of the bird and habitat in which the bird was found or collected. If this band is obtained in Canada the appropriate information should be sent to the Canadian Wildlife Service, Ottawa, Canada.

Migrating birds recognize no political barriers and few geographical obstacles. Banded birds from the Russian Arctic and elsewhere in Europe have been taken in America. Banded American birds have been retaken in Europe, Siberia, Africa, South America, and the islands of mid and southwestern Pacific. Some birds migrate but little, while other species range extensively.

The following table records the number of birds of different groups and species banded in the United States and Canada:

Birds Banded to May, 1954

Ducks, Geese and Swan	1,724,750
Coots	48,000
Gallinules	2,750
Rails	2,800
Woodcock	5,850
Wilson Snipe	1,300
Doves and Pigeons	150,350
Upland, non-migrant Game Birds	41,500
Total Game Birds	1,978,100
Gulls and Terns	1,137,500
Other non-Game Birds	4,743,500
Total non-Game Birds	5,881,100
Total Birds Banded	7,859,200

EXTENT AND RESULTS OF BANDING

That bird banding is popular in the United States and Canada may be seen by the fact that nearly 8,000,000 birds have been banded to date (over 900,000 of these were banded in Canada). From this total there has been over an eight percent return. As would be expected the game species almost always show the highest degree of return. The rate of return by species varies greatly. The harvest from these different groups or species seems to range from about 4 to perhaps 40 percent or more of the population of the species or from a unified segment of the species.

Where sound management is practiced this relatively high rate of harvest need not be alarming. Indeed, there have been more examples of underharvest than over-harvest of game in this country. Information from banding nearly two million waterfowl shows that normally there is an annual turnover of the adult and near-adult population between 60 and 70 percent. Expressed in another way it means that the longevity of between 60 and 70 percent of these birds will be decidedly less than one year.

Such mobile creatures as migratory birds go where they will, and within limits can and do adopt new wintering or nesting grounds, yet as the mass of scientific data accumulates from banding and other sources, we are amazed at the fidelity with which species hold to their ancestral flyways and to their nesting and wintering grounds. With some species these may be thousands of miles apart. Not only do the surviving birds return to almost the exact area where they nested or wintered the previous season, but there is convencing proof that on their migrations they normally follow the same general routes. Some species migrate over broad expanses of ocean. The Pacific Golden Plover, for example, nests along the eastern segment of the northern Siberian coast to Bering Strait and in Alaska along the coast of Bering Sea and Kotzebue Sound. It winters in the Hawaiian and other islands of the central and southern Pacific. Returning individuals are known to go to the same restricted few acres of wintering habitat year after year.

Examples are legion of banded birds being retrapped in the same pond or under the same bush on the wintering grounds or being found on the same acre of marsh during subsequent nesting seasons (Cottam 1951). One banded mallard hen actually used the identical nest site for ten successive years! As an experiment, pintail ducks were trapped during the winter at the close of the hunting season, on Avery Island on the coast of Louisiana. These were banded and promptly shipped in crates, via air, and liberated at Oakland, California; Klamath Lake, Oregon; Washington, D. C.; Cape Cod, Massachusetts; and at St. Paul, Minnesota. It is significant that practically all of the returns from these birds came from the Louisiana point of capture or from some point on the route during fall migration toward Louisiana. Some were re-taken the following winter in the same trap and on the same pond on which they were first captured, despite the fact that they had been shipped in enclosed crates via air to widely separated points of America, hitherto unknown to them. Banding gives positive proof of the birds' deep-seated instinct to cling to their ancestral flyways and wintering and nesting grounds.

Objectives in Banding

The value of bird banding lies primarily in the information it provides on movements of individual birds and on mass movement of species as a whole. The flyway population or approximate totals for various species and their movements in migration can be reliably appraised by the returns of banding a representative segment of the population. Resulting data denote upward or downward trends in numbers, longevity of the species, growth rates, age and sex ratios, life histories, and other facts essential for sound management. Consequently, the annual waterfowl regulations are based to a large extent on facts learned from banding.

These data make possible an understanding of population dynamics and the fluctuations of segments of the total population. Accurate understanding of rapidity of population turnover and the factors that affect it are essential to sound management and conservation of any species. From banding we can gain essential information on flyway populations and migration routes of different species, and the flight patterns and lanes of migration from specific nesting areas. Such studies give us our principal source of information on individual flock and species movements, on the degree of individual and flock wanderings, drifting habits, homing territory, and winter and summer ranges.

We can more properly understand the varied environmental forces that affect these highly mobile migratory birds and arrive at meaningful life equations with the aid of banding (Hickey 1952). Hickey appropriately points out that "Life tables can be applied to tabulations of populations according to age groups. These summaries of the age structure of various species suggest to the geneticist and the evolutionist the rate to which natural selection may cull out mutations or permit them to become dominant. To medical men, life tables often disclose advances and weaknesses in public-health programs. From them ecologists can gauge environmental forces, fisheries workers can estimate future catches, and game managers appraise productivity and hunting regulations."

From returns on banded mallards, Hickey was able to show a correlation between annual fluctuating mortality rates for adult mallards and variations in first season recovery rates. He outlined a method of obtaining the percentage of a banded population killed by hunters and concluded that mallard populations are stabilized by an age ratio of about 0.9 young per adult at the end of the hunting season.

Crissey (1955) in his excellent summary of the use that has been and can be made of a sound banding program appropriately points out the need of a planned program that is statistically sound and designed to give information to specific management questions. He shows the need of banding young and nesters on the breeding grounds and then associating the birds banded with population "index" figures from appropriate breeding ground surveys. This will give information on relative numbers or volume of birds which move along the various migration routes, and it will help to give us needed population data. Crissey shows the limitations that must be placed on past banding programs. He and Bellrose (1955) have shown that between half and two-thirds of the bands recovered by sportsmen are never reported.

Cooch (1955) and Scott (1953) have worked out successful techniques for trapping geese and have improved methods for separating and banding adult and juvenile geese which largely eliminates loss of the smaller and weaker birds resulting from trampling and plucking. As the flightless young and molting adult geese are being herded toward the holding or banding pens, goslings tend to mass at the rear. A man then running through the flock can easily separate the adults from the juveniles. Good retrievers have proved of inestimable worth in trapping flightless young and adult ducks and geese.

Color Leg Banding

The number of color-marking projects for migratory birds, including color leg-banding, color neck-banding and dying of the plumage is increasing rapidly. To prevent duplication and overlapping which obviously would result in chaos, it has been necessary for the respective wildlife bureaus of Canada and the United States rigidly to control the permits authorizing these projects.

For many years colored leg bands of celluloid, fabrics, or plastics have been used to supplement the official aluminum bands. The purpose has been to obtain more and better data on life histories, daily movements, territorial limits and preferences and individual habits and relationships of birds. This information was difficult to obtain through trapping and could better be secured by careful observations made possible with the aid of field glasses in following the color-marked birds. This approach has been used extensively in studying colonial nesting birds such as gulls and terns on the Atlantic and Pacific Coasts and nesting gulls on islands of northern and central Utah lakes. Banding of gulls on Utah Lake gave a 4.4 percent return (Tanner and Beck 1941).

Plastic bands have given variable results in that some are removed by the birds shortly after banding while others last for several years. Balham and Elder (1953) have experimented with a heavy, durable thermoplastic called plexiglass which is a trade name for a rigid acrylic resin. The material can be made in any color which is permanent and is .125 inches in thickness. It is cut to measure 2-¾ x ¾ inches which is the same inside diameter as the No. 8 standard aluminum goose band. Detailed directions for applying the plexiglass are given.

Color-Marking of Broods

In recent years it has become evident that more information is needed on the wanderings and flight lines of ducks, geese, and mourning doves. Aluminum and other similar leg bands cannot be read except with the bird in the hand; therefore, they reveal little more than the point of banding and locality of capture. Consequently, a number of different methods of color-marking adult birds have been tried as a means of learning about local wanderings and precise lines of migrations. Usually these color markings need last but a few weeks or months. This short-term requirement is advantageous in that the same color combinations can be used in following seasons or years.

In recent years improved marking techniques have been developed to give information on movements, migration, life history and ecological requirements or preferences of broods of birds. Hickey (1943) gives a brief history of marking methods. S. A. Nordberg (1942) squirted dye on setting eiders, scoters and mergansers as a means of identifying their broods and studying their movements. Low (1945), in studying young redhead ducks, captured a limited number of young and marked them by gluing feathers to their heads. Leopold, Lee and Anderson (1938) developed a system of attaching dyed chicken feathers to the tails of pheasants for field identification. Edminster (1938) used a similar system with ruffed grouse and Trippensee (1941) developed a method of using plastic plaques for game birds. Moffitt (1942) developed an apparatus for marking birds by means of a buried atomizer which sprayed dye on the birds while on the booming ground. Butts (1930) tested over thirty different dyes and stains on small birds and Vogt (1938) successfully used artist's paints in marking willets. Sowls (1950) tested all of these and other markings on waterfowl including feather-imping, but they were largely unsuccessful. He was more successful in the use of airplane dope coloring. He also used colored bands.

Color marking of broods was put to practical use in connection with the Federal Government's questionable subsidy program supporting drainage of "pothole" water areas in our prairie states and the southern prairie provinces of Canada. There was urgent need to evaluate and classify these numerous small water areas in relation to waterfowl values. For this purpose, Chas. D. Evans (1951) developed a method of marking the young birds by the use of dyes injected into eggs during advanced stages of incubation.

Evans experimented with various brightly colored dyes which dissolved in distilled water slightly below their saturation point and found that Fast Green FCF & Ponceau SX (scarlet red) produced by the Warner-Jenkinson Mfg. Co., of St. Louis, Mo., gave best results. It resisted fading and proved not seriously damaging to the developing embryo. The dyes were carried in the field in 60-mm serum bottles with soft rubber caps along with 22-gauge hypodermic needles. All were carefully sterilized and the coloring material was injected into the egg under aseptic conditions. Collodion was used to seal the eggs after injection. In order to avoid injury to the embryonic membranes, only the tip of the needle was pushed through the egg hole in the shell and the dye was injected slowly in order to prevent overflow. The hatched and colored young remain visibly colored up to seven weeks after hatching.

The techniques of Evans have been further improved by Alex Dzubin (personal communication). He has used more colors and in greater concentration and injected these about one-half inch under the inside surface of the shell into the eggs the day before or at the time the eggs are pipped. This gave 90 per cent hatchability if extreme care was used in keeping syringes sterilized daily.

By such brood color marking, Evans, Hawkins, and Marshall (1950) obtained much basic data on brood movements, brood preferences as to types of water areas, brood cohesion, mortality, and dispersion. Accurate data were also obtained on distances traveled before flight ability developed and preferences of breeding adults for types of vegetative covering and kinds of water areas. In the pothole section of the country, which is the principal nesting ground for waterfowl, water occurs in potholes of various sizes which may be permanent, semipermanent, or of a temporary nature; or water may be found in artificial dugouts as well as in larger lakes.

COLOR-MARKING ADULTS WITH DYES

Early in the 1940's E. R. Kalmbach, in an attempt to pinpoint foci of infection in botulism outbreaks at the Bear River Wildlife Refuge, used various aniline and airplane dyes to mark different parts of the bodies of ducks obtained from different units of the refuge. Probably because not enough dye was applied or the wrong kind was used, these experiments were not very successful. The color marking was too temporary to serve the purpose.

Since that time there have been varying degrees of success with marking or dyeing plumage, beaks or legs of birds. Donald Schierbaum of the New York State Conservation Department, Albany, has written that "We have recently experimented with some 'Day Glo' color painting spray cans that appears promising; it is convenient to use, dries quickly, is very vivid and does not appear to affect the duck. We do not know how long it will last. The manufacturer (Sherwin Williams) indicates it will last one month in direct sunlight, three months inside. On the under side of the wings it may last indefinitely. We are testing it at the present time."

Dyeing of ducks and mourning doves is reported to be fairly successful in Florida, though it appears that the most satisfactory dyes for the purpose have not yet been found. Winston (1955) trapped 583 ducks of several species on Lake Okeechobee, Florida in the spring of 1954 and already returns were reported from many northern and eastern states. Tests at Delta Research Station in Manitoba indicate that airplane dope applied to the feathers of wing and tail can be effective if five successive coats are applied.

Price (1931) used pigment stains and successfully colored California gulls, and Wadkins (1948) performed many experiments in developing techniques for bird coloring.

Color marking of doves has been used most extensively in Florida where it has helped materially in resolving some questions about migration and local movements. According to Winston (1954) two dyes, "Milling Yellow G. S. Concentrate, 250%," and "Crocein Scarlet N Extra" of E. I. Dupont de Nemours & Co., 1706 Spring St., N. W., Atlanta, Georgia, are used. The dry form of the dye is diluted in a pint of acetic acid, one pint of methyl alcohol, and three quarts of water. Several tablespoons of dye are used until the desired color intensity is attained. The body of the bird is immersed or rolled in the liquid stain. Though the solution completely saturates the feathers, they are reported to become normal and fluffy again on drying. Care must be exercised to see that the dye does not get in the eyes of the bird or on skin wounds. Reports indicate that birds so colored are readily recognizable for at least two months, even during the rainy season, and most birds retain at least a part of the dye until their next molt. Patch dyeing was considerably less effective. Red and yellow were found to give the greatest degree of visibility. One may be sure that these uniquely colored birds will be noted and reported.

NECK-BANDING

Experimental work is being done with colored neck bands on geese to determine the time, direction or routes of migration, family and flock unity, foraging range, life history, disease, depredation and homing ties.

Thus far the United States has not authorized neck-banding of ducks in this country except on a very restricted experimental basis, and these preliminary studies indicate that ducks frequently are injured, either by catching the lower mandible in the band or by obstruction of the throat. This, understandably, has resulted in bad public reaction. Efforts to work out better techniques are being taken at the Delta Research Station, Manitoba, at the Ohio Cooperative Wildlife Research Unit and at the University of Wisconsin.

Neck banding has been much more successful on Canada geese than it has been on ducks. Ducks "fight" the bands much more persistently than do the geese and injury resulting from neck-banding of geese is rare and insignificant. The bands are attached just snugly enough to permit the insertion of a lead pencil between the band and the neck. On the basis of extensive testing, Aldrich and Steenis (1955) have offered recommendations for standardizing Canada goose neck-banding.

In 1949 Taber used colored skin tags on pheasants and a little later Gullion (1951) used similar skin tags on coots; in 1951 Helm (1955) used surgical safety pins to attach tags to the necks of geese. All of these were soon torn off. Colored plastic was then sealed to a rubber band and slipped over the head and onto the neck of geese, but this also proved unsuccessful. A neck marker 1½ inches wide by 6 inches long was then developed by Helm by using a strip of upholsterer's fabric, known commercially as Koroseal. This was placed around the bird's neck and the two ends stapled together with a paper-stapling machine or by using clothing gripper snaps. Red, yellow and white were found to be most easily observed and were readily visible to the unaided eye up to 200 yards. When fluorescent enamels and lacquers were applied to the white plastic these were easily recognizable ¼ mile distant with the aid of 8 x 30 binoculars.

Canadian officials felt that good results were obtained by superimposing characters or symbols on the white plastic neck bands (Personal communication from David A. Munro). They found a "Vinyl" paint (obtained from Ault and Wiborg Co., 82 Peter Street, Toronto 2 B, Ontario) best for this work.

New and superior types of neck bands with attachments by snappers and hooks or with expansible material which allows slipping over the head are now available. Many different color patterns can be produced by welding one color plastic on top of another by the use of a hot iron. The plastics Koroseal and Fabrolite both seem to give good results. A feature of neck-bands yet to be determined is their permanence, although indications are that they may last anywhere from two months to two years or even longer.

Banding officials of the Fish and Wildlife Service do not believe that color marking methods are reliable for obtaining information on migratory movements of birds (Aldrich and Steenis 1955). Students of the subject agree that color marking is of most use in solving local problems and that it has but limited application in solving problems associated with long-distance movements. Experience seems to indicate that the number of persons able to report a combination of color markings accurately is very limited and that if incomplete or inaccurate information is reported the resulting data are misleading and unreliable. Numbered bands seem to afford the most reliable information on long-distance movements.

SUMMARY

1. The migratory flights of birds have intrigued the imagination of man since the earliest dawn of history. Old Testament writers gave accounts of it more than 3,500 years ago.

2. Scientific banding started in Denmark in 1899, in the United States in 1902, and in Canada in 1905. Since 1920 all banding has been done under authority and supervision of the Federal Governments of Canada and United States.

3. With minor exceptions all banding of migratory birds is done with numbered bands showing the Fish and Wildlife Service, Washington, D.C., as the return address.

4. 1,978,100 game birds and 5,881,100 nongame birds have been banded from which there has been about an eight percent return. Individual species of game birds show a return of from four to forty percent.

5. Migrating birds tend to return to their accustomed wintering or nesting territory.

6. Banding gives reliable information on mass and individual bird movements, on longevity, growth rates, age and sex ratios, life histories, and it serves as the basis for understanding population dynamics and life equations, and it aids immeasurably in sound management.

7. Color leg-banding, color neck-banding and dyeing of plumage is growing in favor as a means of obtaining more accurate data on life histories, daily movements, territorial limits, ecology, management, depredation, disease, and for many other purposes.

8. Colored plastics are successfully used to neckband geese, but this method has not been successful with ducks. Both ducks and geese are commonly banded with plastic-colored leg bands.

9. Young birds have been sucessfully colordyed by aseptically injecting non-poisonous aniline dyes into incubated eggs about ready to hatch.

10. Ducks and doves have been successfully stained with dyes.

11. Because of the importance of banding and color marking, this work is carefully supervised by the Federal governments of the United States and Canada.

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USES OF MARKING ANIMALS IN ECOLOGICAL STUDIES: MARKING OF MAMMALS; STANDARD METHODS AND NEW DEVELOPMENTS[1]

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The marking of mammals for individual identification is desirable in any study of mammalian ecology, behavior or population dynamics. Completely satisfactory results are seldom obtained, however, partly because the investigator may not be aware of previous work in marking and partly because some of the problems of marking have not yet been solved. Unfortunately, there has been very little research directed toward the comparison of different marking methods and the systematic testing of new possibilities. Instead, each worker reports, occasionally in detail, upon the methods used by him, often neglecting unsuccessful attempts. Thus the literature on marking is largely a series of scattered paragraphs, buried in life history accounts. This information is brought together from time to time in a review which attempts to assess the current status of the field (Ashbrook 1936; Manville 1949). The present report is such a review.

Mammals may be marked for one or both of two purposes: to distinguish individuals after capture in the hand; or to distinguish individuals at a distance. Similarly, they may be marked in one of two ways, in the hand and without handling.

Marking Mammals in the Hand

For marking in the hand there are three general systems in use: mutilation, tagging (or banding or ringing) and coloring. Mutilation involves toe-clipping, tail-docking, ear-cutting, fur-clipping or branding, sometimes in combination. All forms of mutilation share the disadvantages that they maim the animal, so to speak, and so possibly

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[1] Contribution from Federal Aid in Wildlife Restoration Project W-31-R and the Museum of Vertebrate Zoology, Univ. of California, Berkeley.

affect its behavior, or survival. In addition, marks applied by the investigator may be confused with those incurred by the animal in some other way, or, as sometimes happens with ear-cuts, heal over and can no longer be detected. The advantages of mutilation are that marks may be readily applied with a minimum of equipment, a system may be applicable to a long series of individuals and, in the case of some forms, such as branding, the marks may be read at a distance. A standard system for marking small mammals by toe-clipping and ear-punching has been described by Blair (1941) and similar systems have been used on many mammals up to and including the opossum in size (Reynolds 1945).

Ear-clipping and tail-docking both serve to draw the attention to the animal in the field, and so can be used to advantage with other, less conspicuous markers.

Shearing, clipping or burning off the tips of the hairs is especially useful when the hair-base, or underfur is of a contrasting color, as is usually the case. This has been practiced on fur seals (Scheffer 1950), newborn mice (Svihla 1934) and chipmunks (Yerger 1953) among others. This method is useful only until the next molt but has two cardinal advantages—it is easy and painless to apply and it constitutes a good mark for field identification. The possible series, however, is small. This problem was overcome by Chitty and Shorten (1946) who marked their Norway rats with a number drawn out in the pelage with a depilatory. These marks lasted only two or three weeks.

Branding with a hot iron leaves a permanent mark and has been practiced principally on seals (Lindsay 1937; Rand 1950; Scheffer 1950). These brands have been successfully read 5-7 years after application in the Weddell seal (Perkins 1945) and 20 years after application in the Alaska fur seal (Scheffer 1950). In the beaver the flat, scaly tail has been marked by branding (Bradt 1938) and cutting (Hall, Ms.) Bradt found straight-line brands on the tail of the beaver recognizable for four years at least; cuts into the edge of the tail presumably last for life.

Liquid branding fluid, much used for domestic livestock, has apparently not been reported as successful for wild mammals.

The webs between the toes have been punched as an identifying mark in beaver (Aldous 1940) and fur seals (Scheffer 1950). Such a mark is permanent and seldom duplicated in nature, but it is visible only at close range by a person consciously looking for it.

Tattooing has been a standard method for marking domestic rabbits; it is applicable to any mammal with large ears or, as in the case of bats, membranous expanses of skin. Griffin applied tattooed numbers to the wings of bats but discarded the method in favor of banding because the tattoo was laborious to apply, difficult to detect (it was read by transmitted light) and would not lead to the return of a marked bat found by someone other than the investigator (Griffin 1934). However, tattooing is permanent, when properly applied, and might well be used in conjunction with more obvious but less durable markers.

Tagging involves the attachment to the body of the mammal of a piece of metal on which is stamped the identifying number and often an address to which the tag may be returned by the finder. The disadvantage of tags is that they may be lost due to wear, infection or even the gnawing or scratching of the marked animal. The advantages are that they are easy to affix, easy to see, may be returned to the investigator if found and may be discovered after the death of the animal in owl pellets or predator scats or associated with an otherwise unidentifiable carcass.

Tags, usually aluminum or Monel fingerling tags, are applied to the ear in various mammals, often with great success (Scott 1942; Brant, Ms.). However, in some forms ears are small or losses through freezing or tearing are high, so tags are applied elsewhere. Errington and Errington (1937) tagged muskrats by slipping a 5 x 24-mm aluminum tag through two slits in the skin of the back. This has been found most successful with muskrats not over two months, due to the superior regrowth of blood vessels across the strip of skin between the two incisions (Errington 1944). There is evidence that this method is not satisfactory where the water is polluted, due to infection (Takos 1943).

Small bird bands have been used as loose-fitting bracelets around the hind legs of small mammals (Chitty 1937). Such leg-bands have been modified to hold radioactive cobalt, so that the movements of voles could be traced with a Geiger-Müller counter (Godfrey 1954). On some forms, however, leg-bands have been found to cause irritation, swelling, skin puncture and infection (Takos 1943). On some species this may be overcome by causing the band to encircle the Achilles tendon (*tendo calcáneus*) rather than the entire leg. This method has been used on muskrats, foxes, oppossums and skunks (Cook 1943). Even smaller bands have been clamped loosely around a hind toe on squirrels; Linduska (1942) used rounded fingerling tags, a technique which has been improved upon by the substitution of small bird bands. The band is held on by the large toe-pad. Durability is reported to be excellent (Cooley 1948).

Hensley and Twining (1946) used a No. 7 bird band around the base of the tail in the muskrat, but were not able to ascertain how successful the method was.

Bats, also, have been marked with bird bands. Here it has been found that the most satisfactory position is the "distal portion of the forearm" and that if the band is loose enough to slide the bat will not chew it (Trapido and Crowe 1946). Mohr thinks that a fingerling tag in the ear is preferable for bats due to the ease of application and, especially, inspection (Mohr 1942).

At the other extreme of band-size is the metal collar devised by Sheldon for the red fox. This has several advantages: it allows for growth; it is large enough to bear a considerable legend; and it is conspicuous enough to attract the attention of an observer (Sheldon 1949). This marker appears to be of especial utility in those regions where ear tags are lost through freezing. There was no evidence of loss of the markers and one record of retention for one year.

Mammals with large and conspicuous ears which must be identified at a distance may be marked with either a strap or washer type of marker in conjunction with a colored or numbered plastic disc (Thompson and Armour 1954). Care must be taken here, as in all types of marking, that nothing corrodible (such as brass) comes in contact with the flesh and that no pressure be exerted upon the blood vessels, since impaired circulation leads to infection and sloughing.

In marking black-tailed deer it has been observed (by the present author) that if a plastic disc 2″ in diameter is held on the outside of the ear by a rivetted tag going through the ear, the mark has excellent lasting qualities (see below), whereas if a second plastic disc, on the inside of the ear, is incorporated in the marker, the edges of the disc press against the ear and infection and sloughing result. Of nine deer tagged with double discs (one inside and one outside the ear), four were in satisfactory condition when reexamined from 7 to 180 days later, while 5 were infected or had lost their tags when reexamined 68 to 485 days later. Of 19 deer tagged with single discs (outside only), 17 were in satisfactory condition when reexamined 10 to 735 days later, while 2 tags were missing when the deer was examined 8 and 360 days later. The rate of loss of ear-tags is closely correlated with the pressure the tag exerts on the tissue of the ear.

Marten have been marked with plastic tags sewn to the ear with nylon thread (Anton de Vos, personal commun.).

Cattle ear-tags of the strap sort have been used successfully on fur seals, being attached preferably at (a) the hind margin of the fore flipper at the junction of the furred and leathery parts or (b) the hind flipper over the first or fifth digit, proximal to the claws. Tags should be of silver, Monel or stainless steel to avoid corrosion by sea water. Scheffer estimates that, "If duplicate tags are applied, the efficiency at the end of five years should be in the neighborhood of 94 percent." (Scheffer 1950).

Norwegian naturalists have tagged harp and hooded seals with paired discs joined by wires, one wire passing on each side of a tail vertebra (Sivertsen 1941).

An entirely different type of marker was applied by Hensley and Twining to the muskrat. This consisted of ". . . a waterproof plastic button . . . threaded through the loose skin of the back with a flexible steel needle and secured with another button." (Hensley and Twining 1946). This has the advantage of being visible from a distance on a swimming muskrat; there are as yet no data on its durability.

The antlers of the California mule deer have been marked with metal straps (box car seals) so that the antlers could be identified if recovered after shedding (Leopold *et al.* 1951).

Horn is used as an anchor-point in attaching livestock markers and could also be so used in wild bovids.

Sheep-bells, strapped around the neck of trapped white-tailed deer were found by Hahn and Taylor (1950) to be extremely useful in tracing movements. No loss of bells was noted. The collar method could well be used for attaching individual markers.

The coloring of trapped mammals by application of dye to the pelage for later identification has been made the subject of a special study by Anderson. Avoiding the use of poisonous or injurious dyes (in which category many fur dyes fall) he found that in general best results were obtained if: (a) only white fur was dyed; (b) the fur was prepared by cleaning and "killing" before the dye was applied; (c) the dye was hot when applied. This applied to the most successful dyes, which were almost all basic dyes. Dyes applied under these ideal circumstances lasted up to eight weeks or longer (Anderson 1941). Other workers have found fur dyes (which are poisonous) to be much more useful.

Commercial fur dyes, applied cold and fixed with hydrogen peroxide, were used with success by Evans and Holdenried on the Beechey ground squirrel. Of various dyes, Nyanzol 4R (reddish-brown) and Nyanzol D (black) were best. Of 50 animals marked with the black, 15 lost the dye in 30 days, but 6 retained it for 240 days and one for 330 days, indicating that there was considerable variation either in the marking technique or in the molt-schedule of different individuals (Evans and Holdenried 1943). Fitzwater, using Nyanzol A, already mixed with hydrogen peroxide, marked deer mice, chipmunks and red and gray squirrels and found that the dye lasted 4-6 months, until the molt (Fitzwater 1943). Such dyes are useful for mammals of light pelage, but the range of colors is small. The series can be increased by applying spots to different parts of the body.

A general consideration of the literature on marking mammals in the hand leads one to conclude that investigators tend to rely to too great an extent on some one marking method. It would seem a good investment of time to practice multiple marking. Where individuals need not be seen again at a distance a practical system would be as follows: small mammals—ear-tag plus toe-clipping; bats—ear-tag plus forearm band; large mammals—ear-tag plus ear-tattoo, collar, or band around Achilles tendon.

Where mammals must be identified at a distance it would be a good policy to follow the system outlined above in addition to the application of the mark to be seen at long range.

Marking Mammals at a Distance

At various times small numbers of large mammals being fed in winter have been marked with paint by means of an arrow with a sponge at its tip (Young 1946; Altmann and Simon 1952). Marking normally situated mammals by this means is impractical. Advantage might be taken of habitual rubbing-posts, etc. for the application of paint; Altmann and Simon used painted ropes around hay-racks—the elk thrust their heads between the ropes to reach the hay and thereby marked themselves (Altmann and Simon 1952). These paint marks, applied by arrow or by rope, lasted 4-6 weeks, until the molt.

Various mechanical devices, tripped by the mammal to be marked, have been used to project paint or dye. Quay developed a device for marking shrews; this consists of a mouse-trap, one striking arm of which, when the trap is sprung, strikes the rubber bulb of an eye-dropper, forcing out the marking compound (Quay 1948). More recently Clover has developed a deer marker powered by gunpowder. A length of half-inch pipe has at one end a nipple, through which a nail, the firing-pin, slides. A twelve-gauge shotgun shell, loaded with one dram-equivalent of powder, is inserted in the pipe and the nipple screwed on. The hammer is the striking bar of a rat trap. When the trap is loaded the pipe is full of coloring-matter and a trip wire crosses the trail and connects to the pan of the rat trap. When the animal strikes the trip-wire the rat trap is sprung, the striking-bar hits the nail, the shell explodes and the marking compound is propelled as a spray for several feet. The same worker has perfected a multi-shot device powered by compressed gas (Clover 1954).

It is said, among wildlife biologists, that bears have been marked by "bombing" with paint-filled bags from an airplane and also by placing in their paths a paint-filled rubber bag (like a section of an inner-tube) in which holes are punched, so that the pressure of the foot causes paint to squirt out. Printed reference to these has not been found.

Two marking devices have been developed recently for marking moose; they should be equally useful for other large animals habitually using trails. One of these is a pivoted arm, bearing a cup full of marking material, which swings over and deposits this on the animal's back when the trip-wire is struck. The other consists of a paint-filled plastic sack which is suspended over the trail. A rat-trap is fixed nearby in such a manner that when the trap is sprung (by pressure on the trip-wire) a blade on the striking bar of the trap slashes the paint-sack, showering the trail, and animal, with paint (Taber, de Vos and Altmann, Mss.). Paint causes the hair to mat and fall out, so these devices would be best used with dye.

An entirely new approach has been necessary in the marking of whales. A stainless steel tube is fired into the blubber and recovered later in flensing operations (Rayner 1940). It is said that colored nylon cords are sometimes attached to these projectiles to facilitate recovery. Nothing comparable has yet developed for large land mammals, but when one considers the number of lead bullets carried by men and other mammals without lasting ill-effect, the possibilities seem good. Certainly there is a great need for a permanent marker which can be affixed from a distance.

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USES OF MARKING ANIMALS IN ECOLOLOGICAL STUDIES: LABELING ANIMALS WITH RADIOISOTOPES

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Ecological research may be greatly enhanced by imaginative use of radioactive isotopes. It is the purpose of this paper to review a small fraction of the work that has been done of ecological significance, briefly touch on the advantages, disadvantages, and problems of choosing isotopes, and suggest new applications.

ADVANTAGES OF RADIOACTIVE ISOTOPES

Several peculiar characteristics of radioisotopes make them ideal labeling materials for either plants or animals. First, they are not detectable by the senses of animals that may be labeled or by predators that might prey upon the labeled organisms differentially, if a conventional, visual recognition device were used. A second advantage lies in the ease with which these materials can be applied to large groups of animals or plants with a minimal amount of manipulation as contrasted with the laborious tagging of each individual necessitated by other methods. In some cases radioisotope techniques afford methods whereby the organism may not have to be handled, seen, or captured by the experimenter at either end of the operation. Third, because the "tag" becomes a part of the animal labeled, the individual can be recognized throughout the experiment with little danger that the identifying device may be lost. It may be possible that, using the peculiarity of the decay rate of a radioisotope, the different organisms released at different times may be recognized by instrumental means on the basis of the intensity of the radioactivity given off by the "tag."

Techniques in which radioactive isotopes are used are more accurate than observational methods, because the absence of interference from a human observer allows the organisms to react in a natural way. The study can also be extended into time when poor visibility would make observations inaccurate or impossible.

DISADVANTAGES OF RADIOISOTOPES

Contrary to most ecological field experiments, the initial cost in setting up a laboratory sufficiently well equipped to handle radioisotopes is high. The conventional knowledge of chemistry, physics, and physiology of the organism will not suffice in many of these tests because of the peculiarities of the radioactive material and because radiation hazards are present. Official guides to safety in handling of radiocative materials are available as handbooks from the National Bureau of Standards. These publications provide the important information necessary to protect against health hazards. Many other papers on health physics are available, several of which may be obtained from the Technical Information Division, U. S. Atomic Energy Commission. Some of the problems of safety while injecting animals with radioactive materials have been solved by Anthony and Norris (1946), and the techniques outlined by Hansard and Comar (1953) for handling laboratory animals for dosage with radioactive substances point the way toward use of similar methods in ecological research.

The experimenter has the moral responsibility not to create situations of danger to others or to jeopardize the continuity of natural populations. This responsibility automatically eliminates the use of radioisotopes in labeling some kinds of food animals, and high-level releases into noncontrolled situations.

Injudicious labeling of small animals may lead to shortening of life with concomitant doubt as to the normalcy of behavior or movements exhibited while suffering from radiation damage.

Besides added cost and the necessity for acquiring much background information, the additional time necessary in setting up an experiment with radioactivity should not be overlooked.

CHOICE OF ISOTOPES

Choice of an isotope is made on the basis of availability, type of radiation, energy of the emitted radiation, physical half-life, biologic half-life, radiotoxicity, and metabolic characteristics. The type of experiment will dictate the isotope to be used. As a guide for the selection of isotopes for tagging experiments it would be well to study the works of Bugher and Taylor (1949) and Fuller *et al.* (1951), who have discussed, in detail, the problems involved in the selection of isotopes for experiments. Siri (1949) has presented a good discussion of the principles and factors involved in tracer methods. Many sources of information on physical half-lives of isotopes are available, of which the most informative publication (exclusive of the many papers on specific isotopes) is that of Hollander, Perlman, and Seaborg (1953).

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Information on the biological half-life (that time in which an animal is able to eliminate one half of the administered dose by regular processes of elimination) is scattered throughout the literature, but specific data on virtually all the elements are now available. The rate of elimination of an isotope may figure prominently in ecological experiments. This is especially true in aquatic studies where the isotope which is released may be re-absorbed by other organisms and distort the final picture.

Basic radiotoxicity studies have been summarized by Tutin (1949). Many subsequent reports are available on this subject.

As an illustration of the manner in which the above factors are involved in an experiment, the following hypothetical study is presented. The problem is to label mountain sheep on their summer range and follow them to the lowest altitude reached in winter. Since this animal is a game species, an isotope that has a long biological half-life and high radiotoxicity must be eliminated from consideration. Also, an element must be used that will be readily absorbed and largely concentrated in an organ that is not eaten; particularly, no element such as Cs^{137} which is heavily concentrated in muscle tissue may be used. The major portion of the element must be excreted slowly in the urine and feces so that the droppings may be readily identified—a strong beta or gamma emitter is indicated. Radioiodine (I^{131}) most nearly satisfies the requirements, but must be used at low levels since it is relatively radiotoxic because of concentration in the thyroid. The short half-life of I^{131} would limit the study to about one month.

APPLICATIONS IN ANIMAL ECOLOGY

The contributions of entomologists, as summarized by Jenkins and Hassett (1950) and Lindquist (1952), have demonstrated the many applications of radioactive isotopes in animal ecological research. The uses of radioisotopes in studies of the ecology of disease transmission have been reviewed by Jenkins (1954). In this field radioisotope labeling techniques have contributed greatly to advances in medical entomology and numerous new ecological applications are indicated. Strangely, few papers of direct ecological content have appeared that cover other animal groups. Griffin (1952) has used Zn^{65} in aluminum tags and an automatic recording device to study the movements of the semipalmated plover, and has given a good description of the exposure problems involved in such a study. Meadow voles were tagged with leg bands containing Co^{60} (Godfrey, 1954a). This study demonstrated the ability to locate the animals in the field with a Geiger-Müeller tube mounted on a long probe. The same basic method has also been used by Godfrey (1954b) in tracing the movements of moles underground. This type of tagging has many applications.

Jenkins (1954) made a female lemming radioactive by feeding rolled oats spiked with P^{32}. It was found that the animal could be easily identified and located in the field, and its radioactive droppings served to determine its range of movement. The offspring of this animal was also radioactive.

Allied fields furnish perfected methods for labeling animals. Papers in medical and biochemical journals are sources of useful techniques directly applicable to ecological research. Libby and Tubis (1952) have developed a capsule for the oral administration of radioactive substances to humans. A modification of this device should prove of value in studies of fishes or for the easy labeling of reptiles, birds, or mammals, since it could be concealed in food. Modifications of recently developed implantation guns (see advertisement P. IX, *British Jour. Rad.*, **27** (323) Nov., 1954) may be of value in labeling large numbers of animals. A pellet of radiogold or other suitable metal could be quickly and easily implanted in an animal for recognition purposes.

Research into disposal methods for radioactive wastes may reveal usable products which may solve labeling problems. Hatch (1953), for example, has fixed radioactive wastes in small spheres. These tiny radioactive pellets may solve one of the most serious problems of radioactive labeling; *i.e.*, the elimination of the label in urine or feces. Such pellets, implanted intramuscularly or subcutaneously, would be eliminated slowly, thus providing a longer lasting "tag." In reptiles and amphibians, injections of small quantities of beta-emitters in different parts of the body might be used as a code for recognition of individuals.

Many nutritional and metabolic studies with animals have been carried out which suggest the use of radioisotopes for certain ecological problems. The length of time that radioactive materials can be identified in feces and urine is one by-product of such studies, which may be of value in ecological research. By applying such information to experiments in big-game biology, it is theoretically possible to determine that big-game animals from a given drainage basin moved to a particular winter range on the basis of analysis of the droppings within the winter range area.

Brazda (1953) has pointed out some of the problems involved in tracing the exact routes of migratory big game. By labeling with radioactive materials, several of the more difficult problems, such as the capture of animals before and after the migration, might be eliminated. This system of identifying droppings has several other possible applications including the tracing of migration routes of birds, delimitation of home ranges of rodents and birds, positive identification of predators, and establishment of boundaries of foraging ranges. Finkel (1947) has found that fission elements move across the placenta into the unborn young. This transference, which has since been confirmed for some other radio-elements, offers a possible method for the identification of specific litters in rodents and other mammals.

Virtually the entire animal kingdom may be subject to study by radioisotope labeling methods. Predation of ostracods on paramecium has been demonstrated (Pendleton 1952). Several papers have been published on the uptake of radioactive materials in protozoans (Andresen *et al.* 1952, Chapman-Andresen and Robinson 1953), and from these basic studies it is possible to visualize numerous micro-ecological studies.

The insect-plant relationships of a specific plant have been traced (Pendleton and Grundman 1954), and it is suggested that this method of labeling the plant and checking the insects found on and near it may have further application in studies of agricultural plants and insect pests. Cornwell (1955) stated that the artificial release of labeled insects in the field is unsatisfactory for vector studies and advocated direct labeling from the radioactive plant. The technique of Arnason, Irwin, and Spinks (1950), who inserted cobalt wires in wire worms and found that they were able to follow the insects under several inches of soil, is applicable in studies of amphibians, reptiles, and fishes. Thus labeled, a probe location arrangement similar to that used by Godfrey (*op. cit.*) could be employed to find individuals. With this type of labeling, migration ranges, daily movements, and home ranges could be defined.

Employing the many methods for labeling insects summarized from the literature by Jenkins and Hassett, and Lindquist (*op. cit.*), food studies of fishes, amphibians, reptiles, birds, and entomophagous mammals can be studied with great accuracy. The relative efficiency of predation by any species on any suspected pest may be determined in this manner, since large numbers of prey species can be made radioactive for such studies. The extent of predation by flycatchers on apiaries, as one example, might be accurately detemined by making colonies of bees radioactive through labeled honey or syrup. By taking the flycatchers in the area, some index of predation on the colony could be obtained.

Determination of food habits in fishes is particularly amenable to study with radioactive materials, because virtually all of the smaller organisms taken as prey can be made radioactive. Pendleton and Smart (1954) found that fry of one species of fish have greatly varied abilities to obtain foods in the form of small crustaceans. Counts on some fry indicated that 80 or more ostracods had been taken by some individuals while, within the same group of fry, others had taken only one and some none. This information might suggest one of the reasons for the tremendous losses in young fish at the fry level. Studies of the uptake of phosphorus in trout (Hayes and Jodrey 1952) showed that 66 per cent of the initial injected dose was retained after 52 days. This labeling technique should be of value in studies of nonfood fishes and in any controlled situation where no hazards would be produced.

It is possible that the addition of radioactive isotopes to internal plastic or metal tags now used might facilitate their location when fishes have been captured. However, the numerous tagging methods employed in fishes contra-indicate the use of radioactive labeling unless considerable additional information can be obtained, or unless radioactive labeling methods can be worked out to increase the percentage of "tag" retention in the fish. Gerking (1953) has studied the evidences for home ranges in stream fishes. Perhaps further studies of this nature may be carried out with radioactively labeled fishes.

Kritchevsky *et al.* (1951) studied the distribution of C^{14} in an egg after feeding labeled food to the adult. Labeled eggs have applications in upland game bird and waterfowl management. Use of C^{14} is not advised because of low-energy beta emissions, but Sr^{89} or P^{32} should prove transferable and thus aid in identifying nests of birds feeding in a baited area.

CONCLUSION

Although radioisotopes are useful for some investigations that have hitherto been largely impossible, they are not in all cases better than many of the conventional methods already well established. Because of increased hazards, radiotracers should be used with caution and only in those studies where they are superior to the conventional methods. However, they offer great promise for many studies where no satisfactory methods have as yet been discovered.

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EFFECTS OF WATER FLUCTUATION AND VEGETATION CHANGE ON BIRD POPULATIONS, PARTICULARLY WATERFOWL[1]

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INTRODUCTION

In recent years reclamation activities in the Columbia Basin of Washington have resulted in profound changes in the character of the entire landscape throughout this region. The present study is an attempt to clarify some of the biological effects of impoundment behind O'Sullivan Dam in the Potholes area, Grant County (Johnsgard 1955b).

In this area, a large expanse of moving sand dunes and a high water table are responsible for causing the formation of numerous small water areas, or "potholes," between the dunes. The physical nature of the area and its limited potentialities have made it of little value to man in the past, and it has only been subjected to grazing. Except for this influence the area remained almost undisturbed until the completion of O'Sullivan Dam and the formation of Potholes Reservoir. The reservoir has flooded many of the potholes and has materially raised the levels of those remaining. The objective of this study is an attempt to correlate these water level and vegetational changes with changes in avian populations, thus providing a means of predicting future population changes and population potential.

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[1] Contribution (No. 2) from the Washington Wildlife Research Project, the State of Washington Department of Game and the State College of Washington cooperating.

Ecologic work was begun in the area by Stanley W. Harris in 1950 (1952, 1954). His study provides an indication of biotic conditions before the impoundment caused a measurable effect on the wildlife of the area, and is concerned primarily with waterfowl. Breeding waterfowl of the area were also studied in 1952 by Allen J. Greene, U. S. Fish and Wildlife Service. From June 15 to August 15, 1953, and from February 15 to August 15, 1954, intensive field work for the present study was conducted in the area. Periodic surveys were also made during the fall and winter of 1953.

History of the Area

The Potholes area (Fig. 1) lies in the approximate center of the Columbia Basin of east-central Washington. It is located east of the Columbia River and north of Frenchman Hill, in a shallow depression known as the Quincy Basin.

Lava-flows covered the area, in some places to a depth of at least 4,000 feet, during the Miocene epoch. These flows were later subjected to gentle warping and folding, and were gradually covered with unconsolidated materials from a depth of a few to 250 feet (Bretz, 1928).

During the Pleistocene epoch the melting waters of the Wisconsin glacier spilled over eastern Washington, following the general slope of the land toward the southwest. The evidence of the magnitude of water volume involved and the velocity with which it raged across the landscape is vividly recorded in the present day scabland channels, dry cascades, mid-channel buttes, and other indications of a torrential water flow so great as to stagger the imagination.

The scouring action of this invading water cut through to bedrock on an area of over 2,800 square miles, and buried another 900 square miles in the glacial debris (Bretz 1928). These river channels, the "scablands," originate at four loci in the northern part of the basin. Portions of three of these scabland channels converge and empty into the Quincy Basin of Grant County. The sand that was deposited by these impounded glacial waters covers at least 24 townships and is the origin of the dunes which characterize the Potholes area.

Prevailing southwesterly winds have resulted in the formation of countless crescent-shaped dunes throughout the area. Many of the dunes have joined to form long ridges transverse to the prevailing winds, and range in height to 60 to 70 feet. In general, larger dunes occur where vegetation is almost absent, whereas the semistabilized dunes present a lower and more rounded aspect.

In the early 1900's many ranchers owned small desert claims and grazed herds of cattle throughout the region, especially during the relatively moist years of 1906-1916. At this time a local rancher, Budd McRenolds, estimated the number of potholes to be at least 2,500. Beginning about 1916 a series of dry years forced most of the settlers into bankruptcy; the desert claims were abandoned and many of the people put on relief. According to local residents the lowered water table caused many of the tule-lined potholes to dry up and be replaced with saltgrass flats (Budd McRenolds, personal communication).

In contrast to the estimated 2,500 potholes of the early 1900's, a count based on aerial photographs made in 1949 revealed 889 potholes. The filling of Potholes Reservoir has further reduced this number by flooding, so that the present number is estimated at 400 to 600. Since new potholes resulting from a higher water table have not formed as rapidly as the old ones are being flooded, further reduction appears likely.

Construction of O'Sullivan Dam was begun in 1947 and was completed in 1951. The dam is earthfilled, rock-faced, about three and a half miles long, and has a maximum height of 207 feet above bedrock (1,059 feet above mean sea level). The impounded water will cover a maximum of about 30,000 acres and have almost 250 miles of shoreline. If raised to its proposed maximum elevation, 1,052 feet, it would coalesce with Moses Lake and raise its level about five feet. The reservoir is being raised approximately five feet per year, and maximum levels will likely be reached by 1958. Maximum depths of 130 feet will occur near O'Sullivan Dam; maximum annual fluctuation will be about 19 feet. The purpose of the reservoir is to impound waste water from the northern part of the irrigation project for storage and re-use in the southern part. (The above data on the dam and reservoir were obtained mainly from the U. S. Fish and Wildlife Service and the State of Washington Department of Game, 1953).

Climate and Vegetation

Lying in the rain shadow of the Cascade Mountains, the Columbia Basin has a summer-dry climate and low total annual rainfall. Daubenmire (1942) concluded that "semidesert" is the most appropriate term for this region. Approximately two-thirds of the total precipitation falls during the six-month period October through March, reflecting the influence of an oceanic climate. A forty-year record of precipitation at Ephrata, Grant County, indicates an annual average of 7.9 inches (U. S. Dept. of Commerce, 1955), ranging from an average of 1.0 inch in January to 0.2 inch in July.

The area of study is located in the region designated as the Artemisia-Agropyron zone by Daubenmire (1942). The climatic climax is dominated by *Artemisia tridentata* Nutt. and one of the conspicuous grasses is *Agropyron spicatum* (Pursh) Scribn. & Smith. *Chrysothamnus nauseosus* (Pall.) Britt. and *C. viscidiflorus* (Hook) Nutt. are present in sandy sites such as the Potholes area. In the area of intensive study *Oryzopsis hymenoides* (Roem. & Schult) Ricker and *Psoralea lanceolata* Pursh dominate those parts of the dunes which are above the direct influence of the water table.

Proceeding southwesterly into the direction of the prevailing winds there is a gradual stabilization of the sand dunes, an increase in plant species present and a higher percentage of vegetational cover. Along this northeast to southwesterly gradient the following three areas were selected for study (see Fig. 1):

Area I—This area of active sand dunes has little or no plant coverage. Potholes show little indication of shoreline vegetation, and the few species present appear to be the first invaders in primary succession. A shrub zone is usually not present (Fig. 2b).

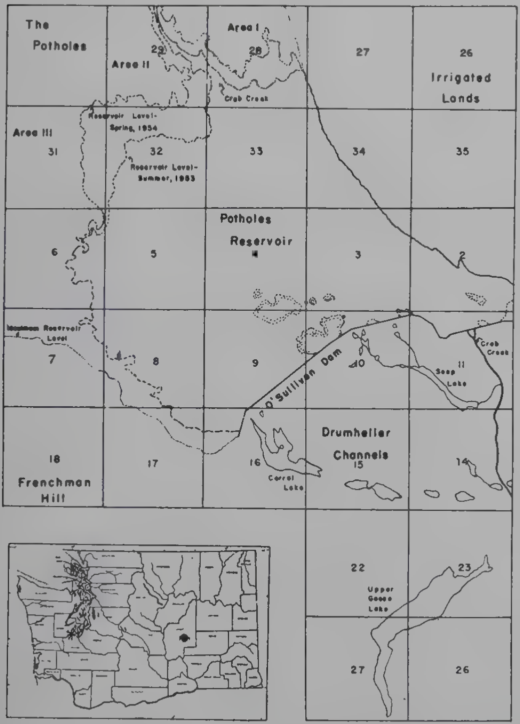


FIG. 1. Potholes Reservior and adjacent area, Grant County, Washington.

Area II—This is a transitional area having many active dunes, but most dunes are semi-stabilized. Potholes generally have a well-developed shoreline vegetation and emergent vegetation is fairly well developed. A shrub zone is normally present and well developed (Figs. 2a, 2c, 2d).

Area III—This is a semistablized area, having few active dunes and a relatively wide variety of both terrestrial and aquatic vegetation. Potholes have a well-developed shoreline and emergent vegetation, with the shrub zone often "capping" the dunes (Figs. 2e, 2f).

Under original conditions the potholes occurring in each of these areas were probably of uniform ecologic character, undergoing only minor yearly coincident water level fluctuations with the underground water table. Thus a distinctive stratification of plant life developed, as each species became established in that portion of the zonation pattern which placed it in its most favorable moisture relationship. Under these conditions perennial shrubs such as rabbitbrush, *Chrysothamnus nauseosus* and *C. viscidiflorus*, became an important part of the vegetational mosaic, forming, with *Bromus tectorum* L., an irregular zone about one to three feet above the permanent water level (referred to as the Bromus-Chrysothamnus zone). Below this zone, and bordering the pothole, a dense cover of salt-tolerant species, mainly saltgrass, *Distichlis stricta* (Torr.) Rydb., and sedge, *Carex douglasii* Boott. occurred (the Distichlis-Carex zone). Above the Bromus-Chrysothamnus zone the more xeric environment allowed growth of only those species such as *Psoralea lanceolata* and *Oryzopsis hymenoides* (the Psoralea-Oryzopsis zone).

The original, undisturbed potholes supported dense stands of rushes, *Juncus balticus* Willd., bulrush, *Scirpus acutus* Muhl. and *S. americanus* Pers., and submerged aquatic vegetation. Harris (1954) has described in detail the typical aquatic vegetation of these potholes.

Willow trees, *Salix* spp., often occur near the potholes, but are not restricted to any part of the zonation pattern.

Underground seepage from the high water levels of Potholes Reservoir has disrupted this zontation scheme. Pothole water levels have become modified, the degree of change varying with their distance from the resorvoir. As a result of these changes several "types" of potholes have developed which, in order of decreasing modification, are defined as follows:

Type 0—These are potholes which became temporarily inundated, and a part of Potholes Reservoir, during spring high-water levels. During the summer drawdown of the reservoir these potholes once again became separated from the reservoir. This pothole type was readily recognizable, not only by the occurrence of lake fish (*Cyprinus carpio, Cottus asper* and *Ameiurus nebulosis*) but also by the lack of shoreline and most emergent vegetation except *Typha latifolia* L. These potholes usually contained an abundance of dead, inundated rabbitbrush (Fig. 2a).

Type 1—These are potholes which are either newly formed, or if present previously all emergent and shoreline vegetation has been inundated. They are characterized by an abrupt transition from the water's edge to typical dune vegetation and lack all emergent aquatic vegetation. Newly formed potholes are easily recognized by the clarity of their water as opposed to the tea-colored water of older potholes (Fig. 2b).

Type 1a—These are potholes which are newly formed over depressions which had previously been covered with rabbitbrush (Chrysothamnus) and associated vegetation. They could be recognized by their shallowness, lack of aquatic vegetation and abundance of dead rabbitbrush standing in the water (Fig. 2c.)

Type 2—These potholes have been subjected to a rise in water level sufficient to flood most emergent vegetation, generally not great enough to inundate the entire shrub zone around the pothole. They are characterized by dead shrubs (mainly Chrysothamnus) along the shoreline, with few or no emergent aquatics (Fig. 2d).

Type 3—These potholes have not had a rise in water level sufficient to inundate the emergent vegetation or the shrub (Bromus-Chrysothamnus) zone, but enough to flood the lower shoreline vegetation (Distichlis-Carex zone). They are characterized by a few flooded shrubs and often show an inner area of emergent vegetation which marked the original size of the pothole (Fig. 2e).

Type 4—These potholes have not been noticeably affected by the reservoir, and have a stabilized and well-defined shoreline zonation with emergent vegetation extending to the shoreline. A Distichlis-Carex zone of shoreline vegetation is present (Fig. 2f).

Forty-seven ten-meter transects were staked out in the three areas and the vegetation analyzed during the second week of July, 1953. Each transect consisted of 20 contiguous 0.2-meter by 0.5-meter plots, from which coverage and frequency were determined. An approximate ten-foot rise in water levels of Potholes Reservoir during July and August of 1953 completely inundated all the vegetational transects established that year. In the spring and summer of 1954 the reservoir level was lowered and the transects were again exposed. Of the original 47 transects, stakes marking 25 escaped destruction. These transects, consisting of 500 plots, were again analyzed at the corresponding time to which they had been studied in 1953.

On the basis of the changes found to occur during this interim, the following conclusions were made:

All species representative of the Psoralea-Oryzopsis zone appeared to be intolerant of prolonged submergence. Plants typical of this zone (*Psoralea lanceolata, Oryzopsis hymenoides* and *Oenothera pallida* Lindl.) which appeared in the 1954 transects were all seedlings; none represented those of the previous year.

In the Bromus-Chrysothamnus zone four species (*Chrysothamnus nauseosus, C. viscidiflorus, Bromus tectorum* and *Spartina gracilis* Trin.) were completely removed from the vegetational matrix. *Bromus tectorum* reestablished itself in a prominant zone directly above the level marking maximum height of water levels, but the other three species were entirely eradicated. Annual forbs and grasses typical of the Bromus-Chrysothamnus zone (*Lactuca scariola* L., *Hordeum jubatum* L. and *Corispermum hyssopifolium* L.) reinvaded the transects, reaching their best development on previous Psoralea-Oryzopsis zone levels.

In the Distichlis-Carex zone changes were somewhat less extreme. *Distichlis stricta* survived submergence very well; in this zone it regained an abundance by July of about half its original coverage. Abundance in the higher zones was greater than before flooding; this resulted from rhizomatous growth and, to a lesser extent, seedling development. However, *Carex douglasii* was greatly reduced in abundance; seedling development appeared responsible for its presence in the 1954 transects. Annual grasses such as *Polypogon monspeliensis* (L.) Desf. and *Panicum capillare* L. were readily reestablished in the transects, although the perennial *Muhlenbergia asperifolia* (Nees. & May) Parodi was apparently removed.

In addition to the decrease, increase, or locational changes of the original species, several species not typical of the Potholes vegetation were noted in the 1954 transects. These included *Heliotropium curassivicum* L., *Chenopodium rubrum*

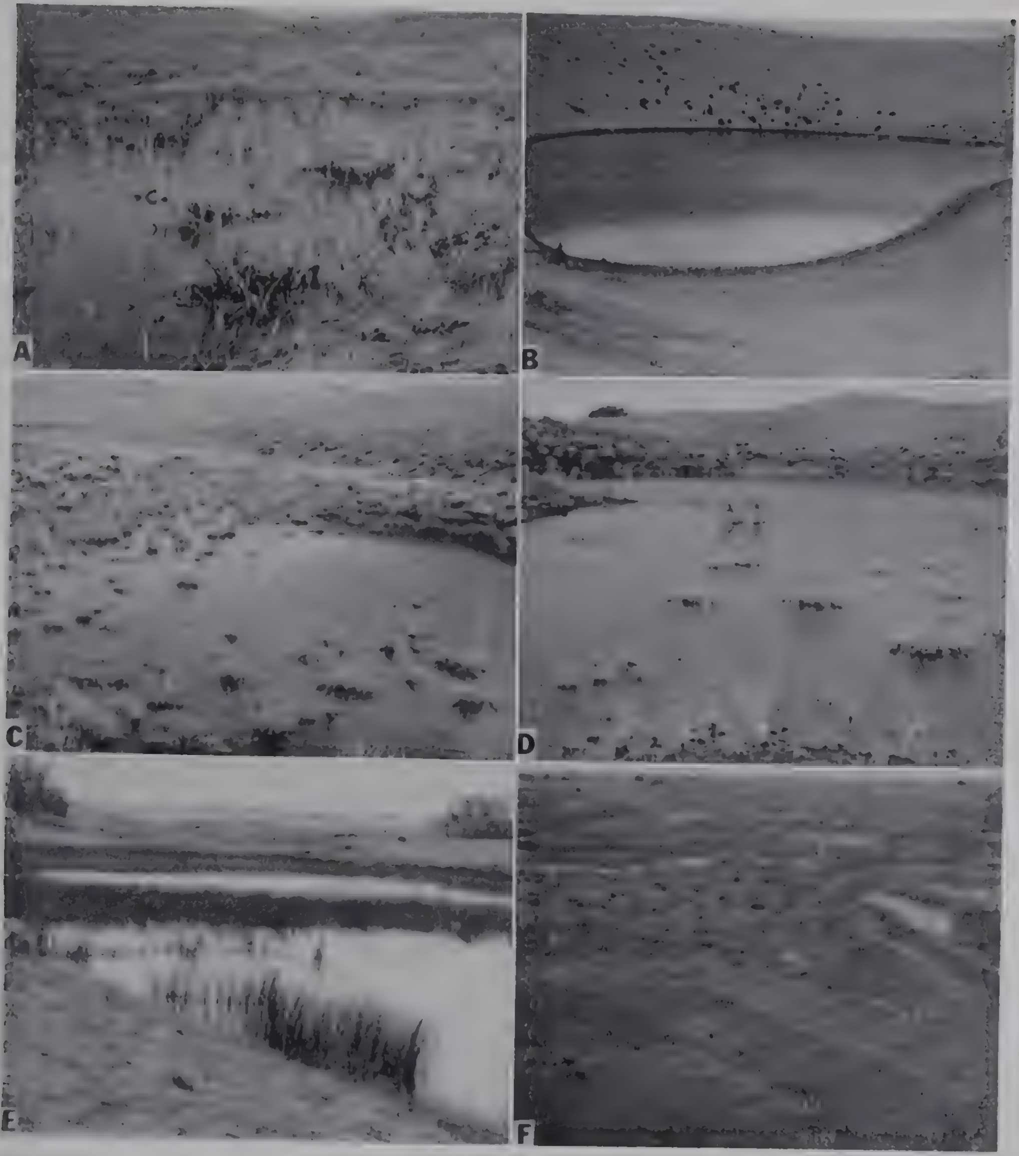


FIG. 2.

2a. Type O pothole, Area II. Note abundance of flooded Chrysothamnus. *Typha latifolia* is the only emergent species present.

2b. Type 1 pothole, Area I. Note lack of shoreline and emergent vegetation.

2c. Type 1a pothole, Area II. The numerous flooded shrubs are characteristic, as well as the lack of emergent aquatic vegetation. The lee slope of the adjajacent sand dune is covered with *Rumex venosus,* which is typical throughout the Potholes area.

2d. Type 2 pothole, Area II. This pothole type has an abundance of flooded Chrysothamnus, and usually some evidence of emergent Scirpus or Juncus vegetation.

2e. Type 3 pothole, Area III. Notice the stabilized character of the surrounding dunes. This pothole type has few or no flooded shrubs and a fair amount of emergent aquatic vegetation.

2f. Type 4 potholes, Area III. Stable water levels and a well-defined shoreline zonation are typical characters of this pothole type. The lightest-colored zone is Distichlis-Carex; the Bromus-Chrysothamnus zone has covered the dune crests.

L. and *Xanthium strumarium* L., all common irrigation weeds which no doubt entered Potholes Reservoir through the irrigation wasteways. *Polygonum persicaria* L. was also observed in several locations. These and other species of weedy nature will doubtless increase in abundance as irrigation is intensified and the reservoir fluctuation becomes greater.

AVIAN DISTRIBUTION

Sample potholes were selected for study and visited at regular intervals during the summer of 1953, and the spring and summer of 1954. Each route was surveyed from two to three times per week. During this survey all birds observed were recorded and assigned to the pothole on or about which they were seen. Terrestrial birds were assumed to be associated with the pothole nearest the vegetation in which the bird was seen. The small size and elusiveness of certain species during the breeding season precluded recording all birds present. However, it is believed that nearly all waterfowl and shorebirds were recorded, as well as most of the passerine and other species not directly associated with the potholes themselves.

Since sufficient typical examples of all pothole types did not occur in all areas, the most adequate bird distribution data for each area (indicated by Roman numerals) and pothole type (indicated by Arabic numerals) are presented (Figs. 3 and 4). Species showing similar distributional tendancies have been grouped together in these charts, and abundance has been calculated by dividing the number of observations per pothole type into the total number of individuals of a given species recorded for that particular area and pothole type. Data for Type 0 potholes are from Areas II and III combined; because this pothole type has such a distinctive history and extreme modification from the others it has been separated from them by a double line (Fig. 4). The lack of spring data for Type 4 potholes resulted from the high reservoir levels at that time, which greatly affected all pothole levels within distances. Lowered reservoir levels and an expanded route facilitated obtaining data for this pothole type during the summer. A discussion of each of the major species' ecologic status follows; additional information on relative bird abundance in the area has been published (Harris and Yocom 1952; Johnsgard 1954).

The pied-billed grebe (*Podilymbus podiceps*) is a common summer resident in the potholes; records were obtained for all areas and pothole types. The data suggest that its highest abundance is reached on pothole Types 3 and 4, and it is probably more prevalent on the dense, overgrown Type 4 potholes than is apparent. Broods were observed on all but Type 1 potholes, indicating an unexpected adaptability to adverse nesting conditions.

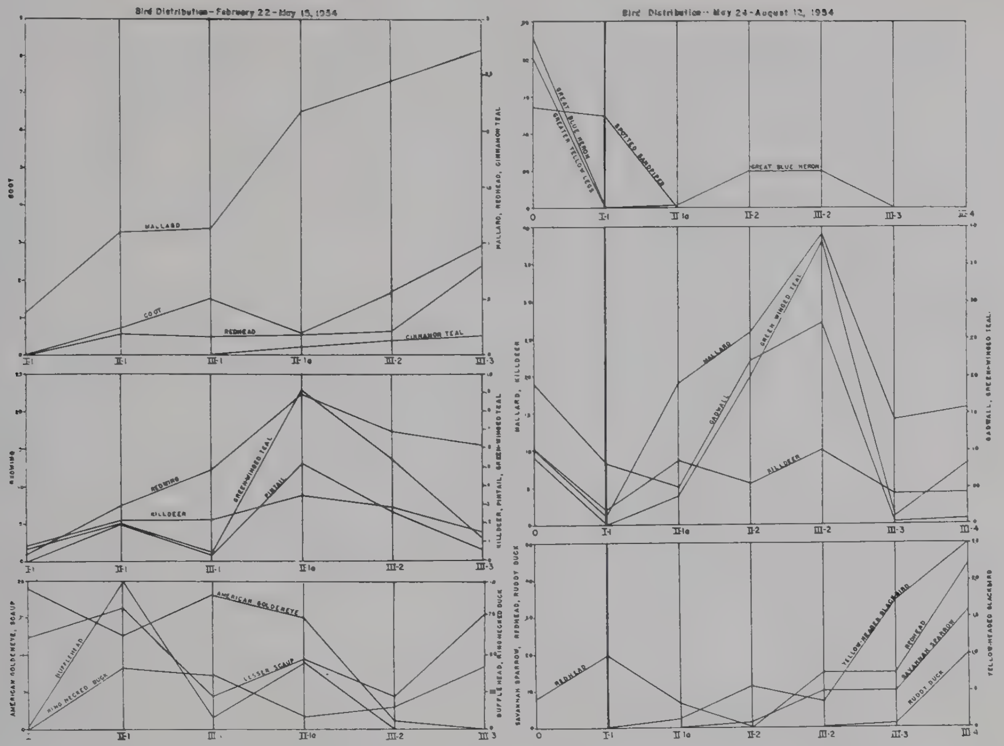
The great blue heron (*Ardea herodias*) is a common permanent resident which nests in large numbers at Moses Lake. It was frequently observed along the shoreline of Potholes Reservoir but was uncommon in the potholes. It is most prevalent on Type 0 potholes (Fig. 4) which had recently become separated from Potholes Reservoir and still contained fish which had been stranded in the potholes as the reservoir receded.

The black-crowned night heron (*Nycticorax nycticorax*) is a common summer resident in the potholes and at Moses Lake, nesting on islands in the Columbia River. Distribution patterns are similar to those of the great blue heron; pothole Types 0, 1a and 2 are heavily utilized. These pothole types, with their abundance of flooded shrubs, provide many excellent perches close to the food supply (mainly *Rana pretiosa* and *Ambystoma tigrinum*).

The Canada goose (*Branta canadensis*) is a common permanent resident, nesting on the islands of Potholes Reservoir and in the dune areas. A large part of this species' summer diet consists of *Oryzopsis hymenoides* seeds, the abundance of which is usually impoverished by cattle grazing. Geese often fed in the active dune area (Area I), where cattle rarely graze because of the relative scarcity of vegetation. The comparative seclusion from most other bird and mammalian disturbance may also partially account for their preference of this area.

The mallard (*Anas platyrhynchos*) is an abundant permanent resident in the area. During the spring (Fig. 3), including almost the entire nesting period, the distribution peak occurred on Type 3 potholes but extended over a broad ecologic range of pothole types. However, the summer data (Fig. 4) show a peak on the Type 2 and, to a lesser degree, Type 1a and 0 potholes. The reason is apparent; the flooded shrubs of the latter types provide an excellent shelter in which molting birds can skulk. Brood utilization was also highest for these potholes types. Besides the escape cover provided by the shrubs they seem to provide attraction for insects, and broods were often observed feeding about them.

The gadwall (*Anas strepera*), although never present in large numbers in the potholes, produced almost as many broods as did the ubiquitous mallard during 1953 and 1954. It slowly became evident that most gadwalls had territories along the shoreline of Potholes Reservoir; frequently their



FIGS. 3 AND 4. Relative abundance of representative species on various areas (Roman numerals) and pothole types (Arabic numerals). Spring data (Fig. 3, left) based on 837 pothole observations, summer data (Fig. 4, right) based on 948 observations. Abundance equals total individuals recorded per area-pothole type divided by the total number of observations for that area-type.

territories centered on dune islands and rarely did they include any potholes. Several investigators, including Bent (1923) and Miller and Collins (1954), have reported on the gadwall's proclivity for utilizing islands as nest sites. Thus the vast amount of potential habitat provided by the islands and shoreline of Potholes Reservoir helps account for the large brood production. The summer distribution data (Fig. 4) show that, of the potholes utilized, Types 0, 1a and 2 are used almost exclusively; Types 3 and 4 are almost entirely avoided. This distribution also obtains for brood utilization. Nesting is usually far from water in the Psoralea-Oryzopsis zone.

The baldpate (*Mareca americana*) is an abundant migrant in the region, breeding in small numbers. The limited data suggest that its distributional preferences are rather similar to those of the gadwall.

The pintail (*Anas acuta*) is a common summer resident in the area, showing preferences for Type 2 potholes (Fig. 3). Its distribution pattern remained unchanged throughout the seasons observed, indicating no differences in nesting and postnesting preferences. Possible reasons for this distribution must be speculative; those advanced for the summer distribution of the mallard probably pertain.

The green-winged teal (*Anas carolinensis*) is a common summer resident in the area, with a distribution (Figs. 3 and 4) very similar to that of the pintail. Total brood production for the green-winged teal and pintail dropped considerably in the Potholes area during 1954; both species prefer Type 2 potholes for nesting territories. Drawdown in reservoir levels during the nesting period resulted in most of the Type 2 potholes being transformed into stages resembling Types 3 or 4, and most pintail and green-winged teal deserted their territories. Evidently the decrease in Type 2 potholes was closely correlated with the lower brood production of these two species.

The blue-winged teal (*Anas discors*) is an abundant summer resident in the Potholes area. Its distribution is very similar to that of the cinnamon teal (Fig. 3). Since the blue-winged teal is a late migrant spring distribution data are limited. However the summer data show greatest use of Type 3 potholes by adults and broods. Nesting preferences seem to be important in determining distribution; grasses of the Distichlis-Carex zone, as well as *Bromus tectorum*, are preferred cover. Such cover is essentially lacking in all but pothole Types 3 and 4. The preference of Type 3 over Type 4 potholes may result from the slightly higher water levels which probably influence food availability. Perhaps the greater percentage of open water also has territorial implications to this species.

As is the case with the mallard, there is a definite postnesting movement to Type 2 potholes where adult birds undergo molt. During this period it is impossible to distinguish blue-winged teal from cinnamon teal in the field, thus the two were treated together. Since these two species are relatively late nesters (early May to early August) a rise in water levels at this time might flood many of the nests, which are usually close to water.

The cinnamon teal (*Anas cyanoptera*) is a common summer resident in the Potholes area; its habits and distribution (Fig. 3) closely resemble those of the blue-winged teal. Pothole Types 3 and 4 are preferred by these species for nesting; Types 0, 1 and 1a are avoided. Type 3 potholes were used most frequently by broods.

The shoveller (*Spatula clypeata*) is an uncommon summer resident in the area, and distribution data are limited. The data suggest a distribution peak on Type 2 potholes, although broods were recorded most often on Type 3 and 4 potholes.

The redhead (*Aythya americana*) is an uncommon summer resident in the area, and very few broods were recorded. Distribution data indicate a strong preference for pothole Types 3 and 4, particularly the latter (Figs. 3 and 4). Many females were observed to desert their nests and territories during 1954; this desertion was apparently the result of fluctuating water levels and the negligent behavior characteristic of the species. A few redheads were seen on Type 1 potholes during the summer, but these birds were very likely unsuccessful nesters, for no indications of territorialism were noted.

The ring-necked duck (*Aythya collaris*) is a common migrant in the area. Its spring distribution (Fig. 3) is similar to that of the lesser scaup, showing a bimodal curve with peaks on pothole Types 1 and 3. In general, birds frequenting Type 1 potholes were unmated, whereas those on Type 3 potholes were mostly mated birds. Courtship activities among diving ducks generally occurred on deep and open water, as provided by the bays of Potholes Reservoir and the Type 1 potholes. Following mating, pairs usually moved to the more undisturbed potholes.

The lesser scaup (*Aythya affinis*) is a common migrant in the area. During spring most birds congregated on the larger lakes below O'Sullivan Dam, where courtship activities took place. Spring distribution in the potholes (Fig. 3) is similar to that of the ring-necked duck; possible explanations have been advanced in the discussion of that species.

The American goldeneye (*Bucephala clangula*) was observed in large numbers during the spring of 1954. The distribution patterns of the three species of *Bucephala* are unique and remarkably similar. A definite peak of abundance is found on Type 1 potholes; pothole Types 2 and 3 are almost entirely avoided by these species (Fig. 3). As with the other diving ducks, courtship usually occurred on Potholes Reservoir, lakes below O'Sullivan Dam, or on Type 1 potholes, presumably because of the large area of open water required for the frequent dives, chases, and other displays typical of these species (Johnsgard 1955a). However, in contrast to the ring-necked duck and lesser scaup, there is no utilization of Type 3 potholes. This appears to result from the fact that mated, nonmated and sexually immature goldeneyes and buffleheads tend to remain in groups. Such behavior made it practically impossible to determine the extent of mating, since all actively participated in courtship display.

Only a few records for the Barrow goldeneye (*Bucephala islandica*) were secured. However, in habits, courtship, and distribution it appeared very similar to the American goldeneye.

The bufflehead (*Bucephala albeola*) is a common migrant in the Potholes area, with habits and spring distribution that are closely similar to those of the American goldeneye. Its apparent intolerance of pothole Types 2 and 3, and abundance of Types 1 and 1a (Fig. 3) was one of the most striking examples of habitat selection observed during the study.

The ruddy duck (*Oxyura jamaicensis*) is an uncommon summer resident in the Potholes area, restricted to the most remote and undisturbed Type 4 potholes (Fig. 4). During the spring of 1954 huge flocks congregated on Potholes Reservoir, but not until late May did pairs appear in the potholes. Broods were only observed on Type 4 potholes. As Low (1941) has pointed out, suitable nesting site is of particular importance to the ruddy duck's choice of breeding habitat.

The sora (*Porzana carolina*) is a rare summer resident in the area, occurring mainly on Type 4 potholes. It is apparently somewhat less restricted in distribution than the Virginia rail (*Rallus limicola*), which was observed rarely on the most remote Type 4 potholes. However, it is believed that Type 4 potholes are necessary for the sora's nesting requirements, and that the few observations on other pothole types were not of territorial birds.

The coot (*Fulica americana*) is an abundant breeding resident in the Potholes area. During the spring of 1954 (Fig. 3) the greatest concentrations of migrating birds were found on Type 3 potholes, but distribution peaks occurred on Type 2 potholes during the summer. The reason for this behavior is readily apparent; Type 3 potholes provided the greatest abundance of food for migrants, but the inundated shrubs of Type 2 potholes provided a sturdy and convenient support for nests. Such shrubs might substitute for the emergent vegetation lost to rising water levels, but the inability of the bird to easily adjust the level of the nest to fluctuating water makes this choice of nest substrate a dangerous one. The relatively short nesting period (early May to early July) increases the probability of a high nest mortality during a rapid reservoir rise at this time. Brood utilization was high on pothole Types 2, 3 and 4.

The killdeer (*Charadrius vociferus*), an abundant resident, was prevalent on Type 2 potholes during the spring and summer (Figs. 3 and 4). Lowered reservoir levels during the summer of 1954 caused the formation of numerous Type 0 potholes; killdeers and greater yellow-legs (*Totanus melanoleucus*) utilized these heavily (Fig. 4). Linsdale (1938) noted that the killdeer was associated with habitats that offered both freedom of movement and visibility; most shorebirds observed in the Potholes area exhibited this same behavior. Nesting extends from May to August, thus there is little danger of drastic population reduction caused by flooding.

The spotted sandpiper (*Actitus macularia*) is a common summer resident in the area. It was observed most often about pothole Types 0 and 1 (Fig. 4). A somewhat similar distribution was shown by the avocet (*Recurvirostra americana*), which breeds about Type 1 potholes. Territorial requirements of visibility and unhindered movement may account for its restricted distribution; it was encountered only about this pothole type.

The Wilson phalarope (*Staganopus tricolor*) is a common summer resident in the area and, like most shorebirds, was most abundant on Type 2 potholes. In contrast to other shorebirds however, it was also prevalent on pothole Types 3 and 4. Its preference for grassy nest cover probably partially accounts for this distribution.

The black tern (*Chlidonias niger*), a common summer resident in the area, is restricted almost entirely to Type 4 potholes, where it nests on mats of floating bulrushes (*Scirpus acutus* and *S. americanus*). Other pothole types are apparently unsuited to the species' breeding requirements, and the birds rarely even feed about them.

The mourning dove (*Zenaidura macroura*) is a common summer resident in the area, usually nesting in willows adjacent to, or standing in, the water. Highest populations occurred about Type 4 potholes. The distribution appeared to be determined by available nesting trees rather than the pothole type.

The eastern kingbird (*Tyrannus tyrannus*) is an abundant summer resident in the area, and was most often seen about pothole Types 2, 3 and 4. As with the mourning dove, the presence of willow for suitable nesting sites seems to determine distribution. Willows standing in water are especially preferred.

The western meadowlark (*Sturnella neglecta*), a common resident, has a distribution that appears to be more closely correlated with the area than the pothole type. The species was rare in the active dune area (Area I) but abundant in the semistabilized area (Area III). The bird's abundance appeared unaffected by water level changes, which probably reflects its upland affinities.

The yellow-headed blackbird (*Xanthocephalus xanthocephalus*) is a common summer resident in the area, occurring only in appreciable numbers on Type 4 potholes (Fig. 4). Undoubtedly dense stands of *Scirpus acutus* delineated the nesting distribution of this species in the Potholes area.

The redwing (*Agelaius phoeniceus*) is an abundant summer resident, being most abundant on pothole Types 1a, 2 and 4 (Fig. 4). On pothole Types 1a and 2 it nests on shrubs; on Type 4 potholes it nests in Scirpus, preferring the former. Paralleling the coot it thus modifies its nesting habits to allow for loss of emergent nesting cover. Most nests are placed close to water, the average height of 24 constructed in flooded Chrysothamnus averaged slightly over one foot above water. Thus a slight reservoir rise during the nesting season (mid-May to mid-June) would likely destroy a large pecentage of the nests.

The Brewer blackbird (*Euphagus cyanocephalus*) is uncommon during the nesting season, but large flocks pass through the area during

July and August. The distribution of these wandering flocks is erratic, but often large numbers are seen feeding about pothole Types 1 and 1a.

The Savannah sparrow (*Passerculus sandwichensis*) is an uncommon summer resident in the area. Its distribution (Fig. 4) is restricted, and appears to be closely associated with the Distichlis-Carex zone of Type 4 potholes. Dumas (1950) found it associated with marsh and prairie in southeastern Washington, and Booth (1952) related it to the "Palouse prairie association," both further indicating its affinity for grassy habitats. Where the Distichlis-Carex zone was not present in the Potholes area, this sparrow could not be found.

The vesper sparrow (*Pooecetes gramineus*), a common summer resident, is the most widely distributed sparrow in the Potholes area. It is the only species of sparrow seen frequently in the active dune area (Area I). Its wide occurrence seems attributable to its habit of nesting on the sand, and thus not being dependent on any particular nesting cover. Wing (1949) noted that the vesper sparrow was the only nesting species in the shrub-deficient Agropyron-Poa association of virgin Palouse prairie. Of 13 nests examined in the Potholes area, eight were beneath cover characteristic of the Psoralea-Oryzopsis zone and five were beneath Bromus-Chrysothamnus zone vegetation. This upland location, and the length of the nesting season (mid-May to early August) provides safety from population reductions through flooding.

The Brewer sparrow (*Spizella breweri*) is a common summer resident in the Potholes area, observed most frequently about pothole Types 1a and 2. The species is very closely associated with the presence of Chrysothamnus; all nests observed were built in rabbitbrush, and it was also a favorite perching site. The sparrow's abundance will almost certainly decrease at the same rate as Chrysothamnus in the Potholes area. Kennedy (1914) noted that this species disappeared quickly when sagebrush in the Yakima Valley was cleared for irrigation. Dumas (1950) found the Brewer sparrow associated only with "sagebrush" habitat (*Artemisia* spp. and *Chrysothamnus* spp.) in southeastern Washington. Booth (1952) correlated its occurrence in the Blue Mountains with the "sagebrush association," and considered suitable nest site as the probable limiting factor in its distribution.

An interesting apparent ecologic equivalent of the Brewer sparrow in the nearby Artemisia-dominated loamy uplands is the lark sparrow (*Chondestes grammacus*). Although it was recorded only three times in the sand dune area during the eight months of field work, a fifteen-minute walk through a sagebrush area a few hundred yards away was certain to reveal several of these birds. Attempts to determine the causes for this distribution were unsuccessful, but apparently the physical characteristics of the sand dune vegetation were unsuited to the territorial requirements of the lark sparrow.

In summary, most of the birds studied in the dune environment showed a definite association with a particular pothole type or successional vegetation stage. In some cases this association appeared relatively simple and could be interpreted readily; in others the association was more complex and difficult to interpret. No two species were observed to have exactly the same habitat requirements, which often centered on a single factor such as suitable nest substrate, or several interrelated factors such as food availability, protective cover and territorial requirements. Regardless of the simplicity or complexity of these factors, the environmental changes caused by fluctuating water levels resulted in a redistribution of bird populations throughout the affected potholes. The obvious conclusion is that every bird species becomes part of the biotic community at a particular stage of plant succession and remains a part of that community until the successional stage transcends (or retrogresses below) the tolerance limits of the species.

WATERFOWL POPULATIONS

Yearly brood production provides the best index of the effects of Potholes Reservoir on breeding waterfowl in the area. This is best illustrated by comparing data from potholes of similar sizes, which is presented (Table I) for the five-year period 1950-1954. Although the larger-sized potholes have been inundated, greatly reducing total production, production per pothole on the remaining smaller ones has increased considerably. This accelerated production probably means that breeding birds were forced into the smaller potholes as the larger ones became flooded. It is very unlikely, however, that this increase in nesting density plus additional nesting along the shoreline of Potholes Reservoir will ever attain the production potential previous to impoundment. In both 1953 and 1954 the annual reservoir rise was abnormally late, thus preventing direct loss by flooding. Seasonal occurrence and rate of reservoir rise will unquestionably have a tremendous influence on future waterfowl production in the area. In

Table I. Waterfowl brood production, by size of pothole

Size of Pothole........	1 Acre or Less		2 - 4 Acres		5 - 10 Acres		More than 10 Acres	
	No. of broods	No. of potholes	No. of broods	No. of potholes	No. of broods	No. of potholes	No. of broods	No. of potholes
1950*..................	83	173	35	24	2	2	13	3
Broods per pothole, 1950.......	.48		1.5		1.0		4.3	
1951*..................	134	181	54	7	42	3	22	2
Broods per pothole, 1951.......	.75		9.0		14.0		11.0	
1952†..................	135	190	35	16	28	3	—	—
Broods per pothole, 1952.......	.71		2.2		7.7		—	
1953..................	108	91	—	—	—	—	—	—
Broods per pothole, 1953.......	1.2		—		—		—	
1954..................	114	97	—	—	—	—	—	—
Broods per pothole, 1954.......	1.2		—		—		—	

*Data from S. W. Harris (personal communication).
†Data from A. J. Greene (personal communciation).

normal years the reservoir rise will begin in mid-May and continue through July.

Plants characteristic of the Distichlis-Carex zone provided cover for six percent of the total forty-nine terrestrial waterfowl nests located, the Bromus-Chrysothamnus zone provided 71 percent, and the Psoralea-Oryzopsis zone accounted for 21 percent. Salix, which is not associated with any single zone, contributed the remaining two percent. The importance of the Bromus-Chrysothamnus zone is thus apparent; Chrysothamnus alone provided cover for 50 percent of all the nests found. Since Chrysothamnus is highly vulnerable to permanent destruction by flooding, the possibility of desirable nesting cover becoming a limiting factor in future waterfowl production will be continually increasing.

A comparison of the fall migration of 1953 with that observed during 1951 (Harris 1952) is illuminating. Based on five counts over the area during fall migration, Harris found a total of almost 16,000 waterfowl, whereas about 19,000 were observed in similar counts during the present study. Apparently there is little significance between the total numbers of waterfowl counted and/or estimated to be present during each of the two years.

Far more significant is the great change in species composition observed during the two years. A tremendous increase in mallards, from 29.5 percent of all waterfowl observed in 1951 to 63.3 percent in 1953, is believed to reflect its field-feeding habits. Since it is not dependent on native vegetation for food, the inundation of the original potholes has not had any noticeable undesirable effects on its migratory status. About 85 percent of the food consumed by 37 mallards examined was composed of cultivated crops (corn, *Zea mays,* peas, *Pisum sativum,* and wheat, *Triticum aestivum*), whereas Harris (1952) found that 39 percent of the food of 21 mallards was from this source. Accordingly, species such as the diving ducks, which are not field feeders, suffered from the lack of native food and used the reservoir mainly as a safe resting place during hunting season.

Between 2,000 and 4,000 waterfowl, about two-thirds of which were mallards, were present in the area during the winter of 1953-1954. This comprised approximately ten percent of the total waterfowl present in the Columbia Basin that winter. With the increasing size of Potholes Reservoir it appears that the wintering grounds provided by it will be one of the most important wildlife values of the area in future years. Data from Harris (1952) indicate that few birds wintered in the area previous to impoundment.

In addition to its wintering value, non-game species not recorded previous to impoundment often utilized the reservoir during the spring and summer. Among these were the double-crested cormorant (*Phalacrocorax auritus*) and herring gull (*Larus argentatus*). Western grebes (*Aechmophorus occidentalis*) and white pelicans (*Pelecanus erythrorhynchos*) were also common summer residents on the reservoir.

Ring-billed gulls (*Larus delawarensis*) rapidly colonized the newly formed dune islands of Potholes Reservoir following impoundment, nesting on the sand near the water's edge. During both years of study the reservoir level receded during the nesting season, thus nesting success was high. Since most nests are placed near the water a moderate rise in reservoir level during this time would destroy most of the colony.

Shorebirds of many species congregate along the beaches and islands of the reservoir during migration. Waterfowl, particularly Canada geese, mallards, gadwalls and coots, use the reservoir during the molting period. Numerous colonies of bank swallows (*Riparia riparia*) nest along the sand banks of Potholes Reservoir.

DISCUSSION

Through a synthesis of the data obtained on vegetational changes and their relation to bird distribution and abundance, the following estimate of future bird populations of the Potholes area is possible:

(1) Subject to population reduction through direct nest flooding—Coot, redwing, redhead.
(2) Subject to population reduction through loss of breeding habitat—Blue-winged teal, cinnamon teal, ruddy duck, redhead, Virginia rail, sora, black tern, yellow-headed blackbird, Savannah sparrow.
(3) Subject to population reduction through loss of nesting cover—Brewer sparrow, coot, pied-billed grebe, pintail(?), green-winged teal(?)
(4) Slightly affected by reservoir fluctuation—Gadwall, vesper sparrow, meadowlark, eastern kingbird.

These changes will be effected in several years, when reservoir fluctuations reach their maximum. The rate of population reduction will depend largely on the time of annual reservoir rise; rises occurring during several successive nesting seasons would hasten reduction greatly. Wolf (1955) found that total water level rise during the nesting season was not so important as rise per unit of time.

Species such as the sora, Virginia rail and ruddy duck, which are particularly adapted to and dependent upon undisturbed (Type 4) potholes, will be the first to show the effects of increased fluctuations. As Brock (1914) stated, "A species will show power of adaptation to new conditions in inverse ratio to the perfection of its adjustment to the old. . . ." Similarly, blue-winged teal and cinnamon teal will respond later to the loss of Type 3 potholes. Since Type 2 potholes will be present for several years, pintail and green-winged teal should be present in fair numbers indefinitely. Mallards and gadwalls likewise will adapt themselves to the altered environmental relations very well.

One of the most impressive phenomena observed in the Potholes area was the resilence of most wildlife and vegetation to new conditions caused by flooding. Nevertheless, the net result of all the ecologic changes resulting from water fluctuation will be a decrease in the variety of fauna and flora, with a concurrent population increase of the few very adaptable species. Management under current conditions cannot hope to restore the variety of the original biota.

ACKNOWLEDGMENTS

I am deeply grateful to Dr. Irven O. Buss, Dr. Rexford F. Daubenmire, and Dr. George E. Hudson, all of whom provided many helpful criticisms and devoted much time to my problem. I am indebted to the State of Washington Department of Game and to the State College of Washington for the use of equipment during the field work, and for financial assistance during the entire period of study. I particularly wish to express my gratitude to Dr. Irven O. Buss for his careful reading and editing of my reports and manuscripts.

SUMMARY

Research in the Potholes area of Grant County, Washington, was conducted during 1953-1954 with the primary objective of determining the biotic effects of water fluctuation. O'Sullivan Dam was constructed during 1947-1951; the resulting reservoir has flooded many of the original sand dune potholes and the water levels of those remaining have been materially affected.

Studies were made in three locations, which included an active dune area, a transitional area and a semistablized area. The potholes in each area were classified into six types as to degree of water level change caused by the reservoir, and ranging from Type O (potholes subjected to actual flooding by Potholes Reservoir) to Type 4 (potholes not noticeably affected, exhibiting a stable water level and undisturbed vegetation zonation).

Most bird species displayed a definite association with a particular pothole type or successional vegetation stage. This association could usually be attributed to the presence of suitable nest substrate, protective cover, food availability, territorial requirements, or combinations of these. The environmental changes caused by fluctuating water levels resulted in a redistribution of bird populations throughout the affected area. It was em-

phasized that any bird species remains a part of the biotic community only so long as the successional vegetation stage encompasses the maximum tolerance limits of the species.

Flooding of the larger potholes has greatly reduced total waterfowl production and has forced the breeding waterfowl into the remaining smaller potholes. These smaller potholes have become more productive in recent years, which is probably a result of this movement. Rabbitbrush (*Chrysothamnus nauseosus* and *C. viscidiflorus*) is the most important terrestrial nesting cover for waterfowl in the Potholes area, but is being greatly reduced in abundance through flooding.

Potholes Reservoir has apparently not yet attracted significantly greater numbers of waterfowl to the area during fall migration, although field-feeding species such as mallards are much more abundant than previously. Three-square (*Scirpus americanus*) and saltgrass (*Distichlis stricta*) were found to be important native foods for waterfowl; peas, corn and wheat comprised over three-fourths of the food consumed by all mallards examined.

Attempts to preserve the original wildlife and vegetation of the area would be futile under present conditions of water fluctuation. Those species which are particularly adapted to conditions found in the most advanced vegetational stages have already been seriously affected and will be the first to be extirpated from the area. Only the most adaptable species will be able to persist.

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ADRENOCORTICAL ACTIVITY IN RELATION TO THE DENSITY AND DYNAMICS OF THREE CONFINED POPULATIONS OF *MICROTUS PENNSYLVANICUS*

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INTRODUCTION

This study describes the relationship between population density and adrenocortical activity in the meadow vole, *Microtus pennsylvanicus*, and explores the role played by this relationship in bringing about population declines in fluctuating mammalian populations.

The study was initiated to test the hypothesis, presented by Christian (1950), that high population density constitutes a stress factor eliciting a response from the adrenopituitary system, and thus bringing about the occurrence of the General Adaptation Syndrome (GAS) of Selye (1946). The occurrence of this syndrome in the individuals of a population would constitute a factor limiting population growth and making the population more susceptible to decimating factors.

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In the GAS there are three phases in the reaction of the animals to a stress factor. First is the Alarm Reaction which is elicited by a sudden exposure to a stress situation to which the animal is not adapted. In this stage the adrenal cortex is depleted of secretory products, and the animal shows characteristic symptoms of shock such as hypoglycemia. If the stress situation is continued for a longer period, and is not too severe, a second stage called the Resistance Phase occurs. In this phase the animal has become resistant to the stress situation, this resistance being acquired at the expense of the ability to become adapted to any additional stress superimposed upon the first one. The adrenal cortex is hypertrophied and contains normal amounts of secretory products on a per milligram basis. If the stress situation is prolonged over a longer period of time, or if a new stress situation is superimposed upon the first one, the Exhaustion Phase of the GAS may set in. In this stage the animal is no longer able to maintain its resistance to the stress situation, or situations, and death results. Here the adrenal cortex is hypertrophied with a depletion of secretory products.

If high population density is a stress factor eliciting the GAS it may be expected that the animals of a dense population will probably be in the Resistance Phase and so be more susceptible to other stress factors, such as disease, predation, and adverse climatic conditions, which might not ordinarily constitute important mortality factors for a population. Thus it is of interest to determine the relationship between high population density and adrenopituitary activity.

Various demographic and behavioral characteristics of a population, such as reproduction, litter and adult mortality, maternal behavior, and aggressive behavior, may be related to adrenopituitary activity to a greater or lesser degree and therefore these phenomena are described here in relation to increased population density.

This study consisted of three populations of meadow voles established in large indoor pens and allowed to increase at their natural rates. Blood eosinophil levels were used as the criterion of adrenocortical activity, low levels indicating increased activity (Speirs and Meyer 1949). *Microtus pennsylvanicus* was selected as the experimental animal because it is a species which shows marked fluctuations in population level in nature, and because it may be readily bred under laboratory conditions.

This study was conducted in the Zoology Department, University of Wisconsin, under the supervision of Dr. John T. Emlen, and was supported in part by grant G-3497 (C-C2) from the National Institutes of Health of the United States Public Health Service, and by funds supplied by the Wisconsin Alumni Research Foundation. Housing facilities for the study were provided by the University of Wisconsin Arboretum Committee, and this is Journal Paper Number 29 in the University of Wisconsin Arboretum Series.

METHODS

The three populations of meadow voles were confined in indoor pens which were six feet wide by 25 feet long, and lined with 24-inch-high sheets of galvanized metal. Each pen contained 48 nest boxes whose dimensions were two inches by three inches by six inches. The floor plan of the pens is shown in Figure 1.

The feed consisted of a Rockland Mouse Diet in pellet form, an abundance being provided at all times and supplemented three times a week with fresh greens in the form of lettuce or cabbage. An abundance of water was always present. Litter, in the form of alfalfa hay, was spread on the wood floors of the pens to a depth of about three inches. The mice made runways through the hay and pulled some into the nest boxes. Some hay was also consumed.

The temperature in the building containing the pens was thermostatically controlled during the winter at 65 to 70 degrees Fahrenheit. There was no effective method available for cooling the building during the summer and temperatures of over 90 degrees were recorded for five days of each summer. The pens received fifteen hours of light during each 24-hour period beginning in December of 1953. This schedule was followed to insure reproduction in the populations throughout the year in accordance with Ranson's (1934) observations that *Microtus agrestis* in England required 15 hours of light in every 24 hours in order to maintain breeding activity.

On January 20, 1953, three male and six female meadow voles obtained from Tumblebrook Farm, New York, were introduced into Pen B while three males and six females trapped from fields in the vicinity of Madison were placed in Pen C. The Pen A population was started on March 12, 1953 with three males and five females trapped in the vicinity of Madison. The Tumblebrook

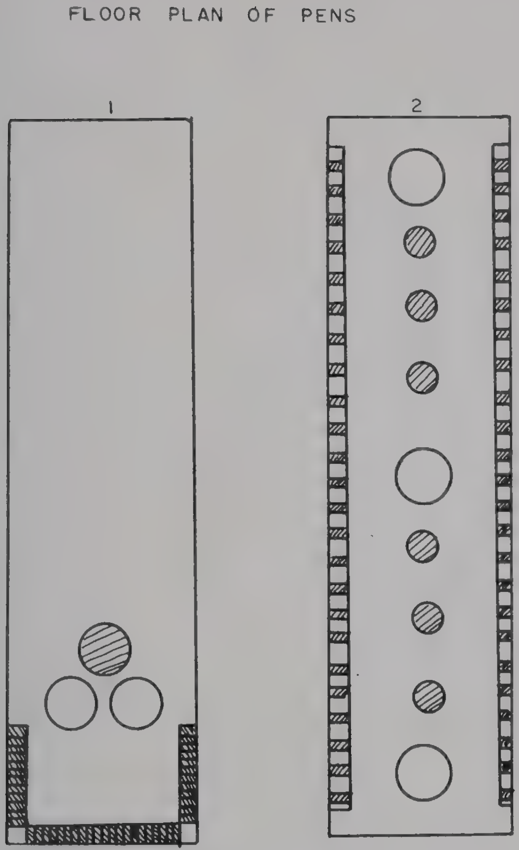

Fig. 1. Floor plan of the Pens. The shaded rectangular areas represent nest boxes. Shaded circles, food pans; open circles, water pans. Floor plan No. 1 is that of Pens A and C while floor plan No. 2 is that of Pen B. Dimensions are given in the text.

mice had been bred in captivity for several generations with considerable inbreeding. All the populations were allowed to grow naturally with no addition or removal of mice being made with but one exception. This exception will be discussed below.

At the end of each month a census check was made in each population. At this time all of the mice were weighed, the weaned young of the month toe-clipped, and the sex, reproductive status, and general condition of each animal noted.

The reproductive condition of the males was determined by the position of the testes; whether scrotal, indicating sexual activity, or abdominal, indicating a lack of sexual activity. The reproductive status of the females was determined on the basis of whether the vulva was perforate or not, a perforate vulva indicating sexual activity. All the animals were examined at each inspection for fresh wounds resulting from fighting, and for evidences of disease.

Two or three times a week the populations were observed for periods of half an hour to an hour and the frequency of aggressive and copulatory behavior recorded. At the same time other aspects of behavior were noted. Every other day the nest boxes were examined for the presence of litters and all new litters recorded along with their estimated age and size. The survival of previously noted litters was also recorded at this time and, in some cases, the movement of a litter from one nest box to another was noted.

Blood eosinophil levels were used as the criterion of adrenocortical activity because the method does not entail killing the animals. It has been known for some time that an increase in adrenocortical activity is accompanied by a decrease in the number of circulating eosinophils, and that this relationship between eosinophil levels and adrenocortical activity is a specific one (Speirs and Meyer 1949; Selye 1950). Louch *et al.* (1953) observed that prolonged exposure to low temperature resulted in an extended depression of eosinophil levels, indicating that this criterion could be used to detect the increased adrenocortical activity hypothesized for the continuous stress of high population density.

Before blood eosinophil levels could be adopted as a technique for measuring adrenocortical activity in *Microtus* it was necessary to determine whether this species had high enough initial eosinophil levels to make significantly large drops possible. It was also necessary to determine the effect of stress upon the eosinophil levels of this species. To accomplish this nineteen adult meadow voles from Tumblebrook were used. An initial eosinophil count was made on each animal, using the method described by Speirs and Meyer (1949), and four hours later a second count was made on the same animals. The mean initial count was 24.2 cells per chamber while the mean of the second counts was 5.2 cells per chamber. The calculated t was 6.603 indicating that the difference between the means was significant at the 0.01 level of significance.

Since previous work had shown a diel eosinophil rhythm in house mice (Halberg and Visscher 1950; Louch *et al.* 1953), it was important to determine the presence or absence of such rhythms in the meadow vole before a schedule of blood sampling could be planned. To obtain the desired information, five male mice were used with counts occurring alternately at four day intervals; a total of twenty counts were made at 9:00 A.M. and 8:00 P.M. respectively, and fifteen counts at 2:00

Table I. Eosinophil levels in the meadow vole in relation to time of day

Mean eosinophil levels		Mean diff.	d.f.*	t	P_t†
9:00 A.M. 27.1	8:00 P.M. 22.7	4.4	38	0.750	0.5
9:00 A.M. 27.1	2:00 P.M. 25.9	1.2	38	0.228	0.9

*Degrees of freedom.
†Probability of t occurring by chance alone.

P.M. The results (Table I) indicate that there were no significant eosinophil fluctuations between 9:00 A.M. and 8:00 P.M. and that all counts made during this period should be comparable. In the population study the counts were made between 9:00 A.M. and 2:00 P.M.

Eosinophil counts were made in the pens at two-week intervals. From eight to ten healthy adult, non-pregnant mice of either sex were caught as rapidly as possible, placed in battery jars, heated under a lamp for five minutes, and blood was taken for counts. The intervals between catching the mice and taking the blood was never longer than thirty minutes in a given pen. Counts for each pen were made on consecutive days to avoid the possibility that disturbance in one pen might effect the eosinophil levels in the other pens.

In April of 1954 the area and number of nest boxes in Pen B was cut in half to observe the effect upon the population growth and eosinophil levels of the populations The pen was restored to its full size in July. The area of Pen C was reduced by half in July of 1954 and returned to its full size in November.

Population Growth Forms

The growth curves (Fig. 2) shows considerable variation between the three populations. Pen B showed a marked population growth earlier than did the other two pens, while Pen C eventually reached the highest population density. Pen A never reached the high population densities achieved by the other two populations. The maximum density reached by the pens varied from 28 animals for Pen A, to 53 for Pen B, and 67 for Pen C.

The conditions which could possibly be related to the variations in population growth may be grouped into two general categories; environmental conditions, and those arising from within the populations themselves. The environmental situation was the same for all of the pens except for the arrangement of the nest boxes and food as shown in Figure 1. However, this condition was the same for Pens A and C yet there was little similarity between the population behavior of the two pens. The environmental conditions played no apparent part in bringing about the varied growth behavior of the populations except that the reduction of the pen area in Pens B and C was followed by marked population declines (Fig. 2).

The different growth forms of the populations were probably dependent upon factors arising from within the populations themselves. In general, these were probably the variable behavioral and physiological responses of the individuals of each population to environmental conditions and the stimulus of increasing population density. This variable reaction of individual animals is illustrated by the work of Crew and Mirskaia (1931) who found a great variability in the response of house mice to confinement in small cages, some animals adapting well to the situation while others showed various manifestations of maladjustment. Strecker and Emlen (1953) and Southwick (1955) found variations in the growth forms of house-mouse populations similar to the ones described here. Brown (1953) also found a great deal of variation in the growth forms of his house-mouse populations.

In the present study some of the variability in population growth can be explained fairly readily. The earlier population growth in Pen B may be explained by the fact that the animals were from a stock of mice bred for several generations in captivity and presumably better adapted to such conditions. Richter (1950) gives evidence that wild Norway rats became "tamer" and better able to breed in captivity after several generations in captivity. The lack of population growth in Pen A during the first seven months of the study is explainable on the basis of a marked cannibalistic tendency on the part of two males making it practically impossible for the young to survive to maturity. The other intrinsic factors that probably played a part in regulating population dynamics are discussed in more detail under the several headings below.

Demographic Characteristics of the Populations

Percent Population Increase. The percentage population increase, representing the net result of the monthly reproduction and mortality in each pen, is plotted against the population density of the previous month in Figure 3. The declining trend in population increase shown by the figure was apparently related to some density-dependent factor or factors arising from the populations. There were a number of demographic character-

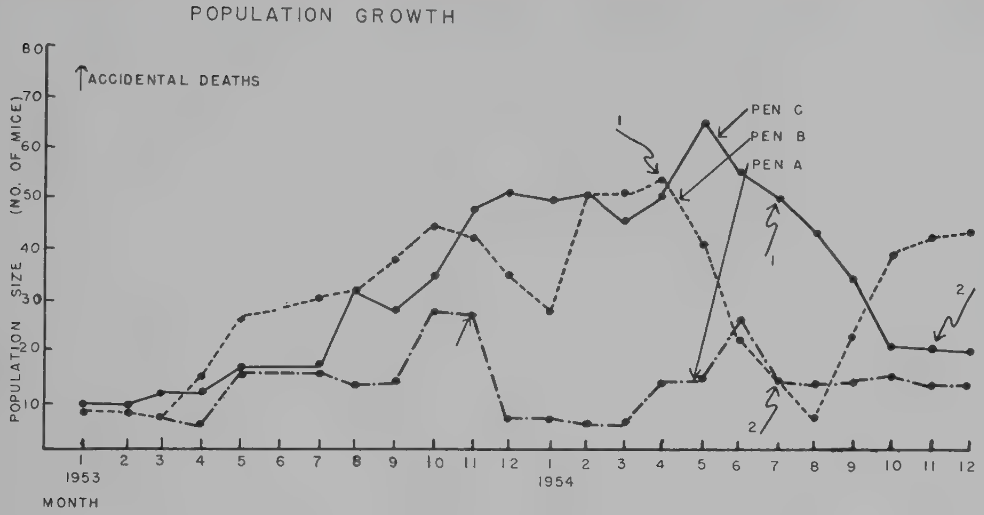

Fig. 2. Population growth for the period of the study. Population size is the number of weaned mice at the end of each month. Curved arrows numbered 1 indicate when the pen space of Pens B and C were reduced by half; curved arrows number 2 indicate when Pens B and C were returned to full size.

istics which may have been related to population density.

Fecundity. Reproductively active mice, those with scrotal testes or perforate vaginae, are referred to in this paper as being fecund. The correlation between fecundity, in terms of the percentage of the adult population that was reproductively active in each month, and the population density for each month is shown in Table II. A significant coefficient of correlation was found in Pen A, but not in the other two pens indicating that a change in fecundity did not always accompany changes in population density. These results agree with those of Southwick (1955) who found a decreased fecundity with increased population density in some of his house-mouse populations but not in others. If the criteria of fecundity used here were reasonably accurate, and autopsy of the animals at the final census indicated that they were, the results obtained in this study are somewhat at variance with those of workers who have found a consistent reduction in fecundity accompanying increased population densities in other species: Pearl (1932) in Drosophila, Pearl and Surface (1909) in hens, Birch *et al.* (1951) in Tribolium, and Kluijver (1951) in the great tit (*Parus major*).

Fertility or Litter Production. The reproductive rate of each population was determined on the basis of the number of nestlings and the number of litters produced per adult female per month. The degree of correlation between population density for each month and litter and nestling production for each month is shown in Table II. It is evident that there was no significant correlation in any of the populations. No attempt was made to record the frequency of pregnancy in the pens hence nothing can be said as to the importance of foetal reabsorption in these populations.

Table II. Coefficients of correlation between population density and various population characteristics

Categories	Pen	r*	n†	P‡
Per cent fecundity	A......	−0.469	19	0.05
	B......	−0.428	21	0.10
	C......	0.128	21	0.10
Nestlings per adult female	A......	0.006	21	0.10
	B......	0.095	24	0.10
	C......	0.405	24	0.10
Litters per female	A......	0.075	21	0.10
	B......	0.108	23	0.10
	C......	0.097	25	0.10
Per cent wounded	A......	0.550	20	0.02
	B......	0.774	19	0.01
	C......	0.704	20	0.01
Fights per mouse per hour	A......	0.129	22	0.10
	B......	0.034	22	0.10
	C......	0.489	22	0.05
Eosinophil levels	A......	−0.676	20	0.01
	B......	−0.557	20	0.02
	C......	−0.598	20	0.01
Per cent adult mortality	A......	0.492	18	0.05
	B......	0.319	22	0.10
	C......	0.587	22	0.01

*The coefficient of correlation.
†Number of sample pairs.
‡The probability of the calculated value of occurring by chance alone; obtained from Table V. A. of R. A. Fisher's Statistical Methods.

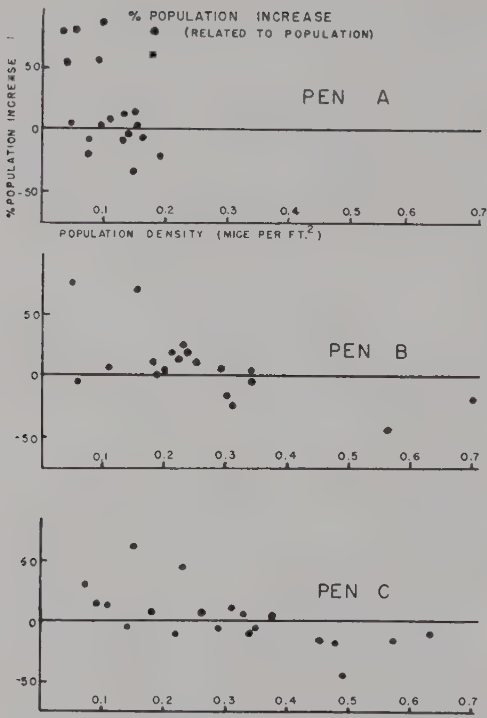

FIG. 3. Per cent population increase. Each dot represents the per cent increase of the population at the end of one month over the population at the end of the previous month.

The number of nestlings per female during periods of population increase was compared to the number of nestlings per female during periods of population decrease. The results appear in Table III and show that there was a slight tendency for smaller numbers of nestlings during periods of population decline. It has been observed in meadow voles (Hamilton 1937), and in muskrats (Errington 1952) that there is a reduced rate of reproduction during decreasing phases of the populations.

TABLE III. Number of nestlings per female during periods of population increase and decrease

	I*	II†	Mean diff.	d.f.	t	P_t
Pen A....	0.78	1.28	0.50	19	1.471	0.20
Pen B....	0.45	1.40	0.86	19	2.118	0.05
Pen C....	0.44	0.72	0.28	19	2.000	0.10

*Mean number of young per female during decreasing phase of population.
†Mean number of young per female during increasing phase of population.

Litter Mortality. Litter mortality, determined in terms of the percentage of young born in each month that failed to survive to be toe-clipped at about three weeks of age, showed a definite threshold, increasing sharply above a given population density in each pen. In Pen B the mean monthly litter mortality was 47% at population densities below 0.29 mice per square foot and 95% above this level. The difference of 48% was significant at the 0.01 level of significance as is indicated by a calculated *t* value of 3.33. In Pen C the mean monthly litter mortality was 52.6% when there were fewer than 0.34 mice per square foot and 97.1% above this level. The mean difference was 44.5% and the calculated *t* was 2.68 which was significant at the 0.02 level of significance. The population density of Pen A never reached a high enough level to show this relationship. This increased litter mortality at the high population densities may have played an important part in population dynamics.

A wide variety of factors was observed to bring about litter mortality. As population densities increased there was a greater tendency for mice to crowd into certain nest boxes that were favored as places to raise litters, thus disturbing lactating females and their young. This disturbance probably brought about the death of the young through trampling, or by inducing aberrant maternal behavior in the lactating females due to emotional disturbances. A probable result of this disturbance was the observation of females transferring their litters from one nest box to another during periods of high population density. At high population densities lactating females were observed killing and devouring their young, and abandonment of litters was common and an important cause of litter mortality. It was also noted that the type of nest constructed by the females changed with increased population density. The normal nest during times of low population density was completely covered while the nests constructed during times of high population density were simply platforms of hay with no covering. Similar changes in nest construction were noted by Southwick (1955) and Brown (1953), and related to litter mortality in house mice. These changes in nest construction may reflect physiological and emotional disturbances in the females building them, or the females of high populations may have been unable to construct covered nests because of the disturbance of other mice; this inability to build a proper nest may itself have resulted in emotional disturbance in the females.

All of the above manifestations of abnormal maternal behavior may be traced back theoretically to a possible shift in the anterior pituitary function brought about by emotional and physical disturbances, and this possibility is discussed in the section on adrenocortical changes in relation to population density.

Another important mortality factor among the young mice was their destruction by adult mice soon after leaving the nest boxes. For a period of several days after leaving the nest boxes the young were very vulnerable to attack by adult mice, especially males. Occasionally young mice would leave the nest box before they were weaned; usually the female would carry them back to the nest box, but sometimes the young would be destroyed by other mice before being rescued. One such case was seen in Pen A where a female attempted, unsuccessfully, to retrieve one of her young from two males who finally killed and ate it.

The observations concerning the causes of litter mortality are general in nature since no numerical data were collected. However, they are similar to those of several other workers. Ranson (1941) noted cannibalism in both sexes of *Microtus agrestis*. Brown (1953) noted that in dense populations of confined house mice nesting females were unable to isolate themselves from the disturbing activities of other mice and this resulted in a decrease in the successful weaning of litters. He found that litter destruction was caused by the nesting females and resulted from the abandonment of the litters, or their being eaten by the females. Linsdale and Tevis (1925) noted that in the dusky-footed wood rat in nature there was a greater tendency for the animals to bunch up under crowded conditions. Southwick (1955) observed a greater tendency for adult mice to crowd into nest boxes containing litters at higher population densities, and found a correlation between this and litter mortality. Calhoun (1949) observed that the period immediately following weaning is the most critical in the life of the Norway rat.

Adult Mortality. Adult mortality was taken as the percent of the total number of adult mice present at the end of one month that were gone by the end of the following month. The coefficient of correlation between population density and adult mortality is shown in Table II and is positive and significant for Pens A and C. The prevalence of mortality was compared to the percent increase in population size for each month to see whether there was any change in mortality under conditions of population growth, population decline and population stasis. The results appear in Table IV and it is apparent that there was a significantly higher rate of adult mortality during periods of population decline than at any other time, thus indicating that adult mortality played a part in bringing about the population declines that occurred following the reduction of the pen space in Pens B and C.

TABLE IV. Adult mortality related to rate of population increase and decrease*

Per cent population Increase	MEAN ADULT MORTALITY	
	Pen B	Pen C
−50% to −11%	30.8%	20.6%
−10% to 10%	3.7%	5.7%
11% to 100%	11.7%	6.7%

Statistical Analysis

I. Difference in mortality between increasing and steady populations

	Diff.	t	P_t
Pen B	8%	1.333	0.3
Pen C	1%	0.389	0.8

II. Difference in mortality between decreasing and steady populations

	Diff.	t	P_t
Pen B	27.1%	5.211	0.01
Pen C	14.9%	3.519	0.01

*Pen A did not have a high enough population level to show the above relationship.

Summary. The demographic characteristics that appeared to limit population density in this study were a high litter mortality at high population densities, and increased adult mortality during the decreasing phase of population change. These factors are discussed in relation to behavioral characteristics and adrenocortical activity in the following sections.

COPULATORY BEHAVIOR

The copulatory behavior of the mice changed markedly with increasing population density. As the density of the populations increased the competition between males for females in estrus appeared to increase. This manifested itself in a number of males, up to five, attempting to mount an estrous female. As a male mounted the female he would be pushed off by another male who would in turn attempt copulation. Thus no male could complete the act of coition. The female would run around the pen with a string of males following her and starting to mount her each time she paused. Eventually the female would retire to a nest box and, facing the opening, prevent the entrance of any males. Normally the act of coition covered a period of about thirty seconds while in a situation as described above no male remained on a female for more than two or three seconds. There was little actual fighting among the males during this behavior; they would simply push and squeak at one another. Occasionally a serious fight would break out between two or more males, and sometimes the female would turn on the males, driving them away. This general type of behavior almost always occurred outside the nest boxes because the females would not remain in a nest box with a group of males.

The behavior showed a definite threshold, occurring in significantly large amounts in each pen only above a certain population level. The data include all copulations and all attempted copulations that were observed, and the term copulation here refers to all mountings including the ones that lasted only two or three seconds. In Pen A there were 0.03 copulations per mouse per hour below a population density of 0.17 mice per square foot, and 0.12 copulations per mouse per hour above this level. In Pen B the threshold level was 0.21 mice per square foot with 0.008 copulations per mouse per hour observed below, and 0.28 copulations observed above this level. The threshold level was 0.15 mice per square foot in Pen C with 0.0 copulations per mouse per hour observed below and 0.25 copulations per mouse per hour observed above this level. Southwick (1955) observed similar behavior in some of his house-mouse populations and related it to a reduced rate of conception among the females so affected. Calhoun (1949) found, in rat populations where the males were not organized into a social order, a type of copulatory behavior similar to that described in this study. He found that females subjected to this type of male activity showed a low rate of conception. In the present study this type of behavior had no apparent relation to the rate of litter production since the latter did not decrease at high population densities. It may have had an adverse effect upon litter survival through its action upon lactating females that were in estrus. Brambell (1939) indicates that there is a post-partum estrus in females of *Microtus agrestis,* while Hamilton (1941) states that in *Microtus pennsylvanicus* an estrous cycle occurs immediately after parturition and some females are capable of conceiving five to six days after parturition. Thus, in the present study, a lactating female could go into estrus soon after parturition and be chased by a number of males while in this state. The disturbance thus created might influence the female to destroy or abandon her litter.

Aggressive Behavior

Types of Aggressive Behavior. Various types of aggressive behavior were observed in the pens from time to time, and could be placed into certain categories. The term aggressive behavior here indicates any type of interaction between two or more individuals resulting in or leading toward fighting.

Mice were frequently observed to defend a nest box against other mice by assuming a position at the entrance of the nest box with the head in the opening and facing outward, thus preventing the entrance of other mice. Another type of aggressive behavior observed was that in which one mouse would chase another away from a particular region of the pen. This chasing was usually preceded by a brief fight after which one of the mice would run. In special cases fighting occurred when a female would attempt to defend her young against cannibalistic adults. Occasionally there were conflicts over a piece of lettuce or cabbage which usually took the form of two mice pulling at a piece of lettuce and did not involve actual fighting. The most common type of fighting was that which involved no apparent goal or purpose. It was apparently brought about by irritation produced by frequent close association with other individuals. In some cases males would appear to seek out other males and attack them. These second males would sometimes run away without fighting but at other times they would fight back. In still other cases a mouse, male or female, would attack any mouse that came close to it regardless of sex or age. Sometimes a fight between two mice would bring about a general excitement in the pen resulting in numerous short fights and chases. Also, at times, the aggressive behavior of one mouse would cause all of the mice in the pen to run to a nest box. Thus the fighting activities of one or two mice could affect the behavior of all the mice in the pen. Similar types of fighting were observed in house mice by Southwick (1955).

Forms of Fighting. The fighting in the pens took a number of different forms. Often two mice would meet and stand facing each other squeaking and making short dashes at each other. Usually one mouse would retreat before actual physical combat occurred, but this behavior was occasionally a prelude to more intense fighting. Often two mice would meet and, standing on their hind feet, push at each other with their front feet. This behavior was usually accompanied by squeaking. Usually one mouse would retreat but sometimes this behavior would lead to a more active form of fighting. The most intense form of fighting involved two mice rolling over and over biting each other. This form of fighting usually lasted only a short time after which one of the mice would run away. It was not accompanied by squeaking. Often a series of these clashes would occur between two mice within a short period of time. Usually the same mouse would retreat into a nest box. This form of fighting often resulted in the mice being severely wounded. A form of aggressive behavior in which one mouse chased another, biting it around the rump and tail, was quite common, and resulted in injury to the pursued mouse. This form of fighting was not accompanied by any squeaking.

Amount of Fighting. The amount of fighting in the pens was determined on the basis of observations made over periods of about half an hour as described in the section on methods. The criteria of fighting were: sounds of squeaking, bumping around in the nest boxes, observed fights outside the nest boxes, and violent chases beginning or ending in fights. The fighting was recorded as the number of fights per mouse per hour. The coefficient of correlation between frequency of fighting and population density appears in Table II and shows that, with the exception of Pen C, there was no significant correlation between all types of fighting, as determined by this method, and population density. These results differ from those of Southwick (1955) for house mice where the fights per mouse per hour increased with population density.

The number of freshly wounded mice at the end of each census period was taken as another indication of the amount of fighting in the pens. Mice of both sexes and all age groups were found wounded indicating that all individuals became involved in fighting at one time or another.

The results of the wound data appear in Figure 4 where the per cent of wounded animals is plotted against population density. Table II gives the coefficient of correlation for this relationship and shows that this is positive and significant for each pen indicating that increased population density was accompanied by increased fighting.

The different results obtained by the two methods of determining fighting probably occurred because of error in the observational method. The observation periods were probably not long enough or frequent enough to obtain sufficient records to show the increasing fighting trend with higher population densities. The more intense forms of fighting may have become more prevalent at the higher densities because of the increased irritability of the mice. Since these forms of fighting were not accompanied by much noise such as squeaking they may have been missed and this may have contributed to the error in the observational data. In this study the number of wounded animals was taken to represent the relative intensity of fighting since there was no conceivable cause, other than fighting, that could have brought about injury to the mice.

The increased fighting was probably indicative of increased disturbance building up in the populations as the population density increased. Calhoun suggests (in Scott and Fredericson 1951) that noncompetitive fighting in rats and mice takes place due to the effort of the individual to obtain undisturbed living space. As the population density increases there will be progressively more disturbance for each individual, this leading to a greater aggressive tendency on the part of the individual. This increased aggressive behavior accompanying increased population density may affect the adrenopituitary mechanism of the animals and thus influence population dynamics as discussed below.

DISEASE

Dead animals, or those close to death, were autopsied for signs of disease. The animals had

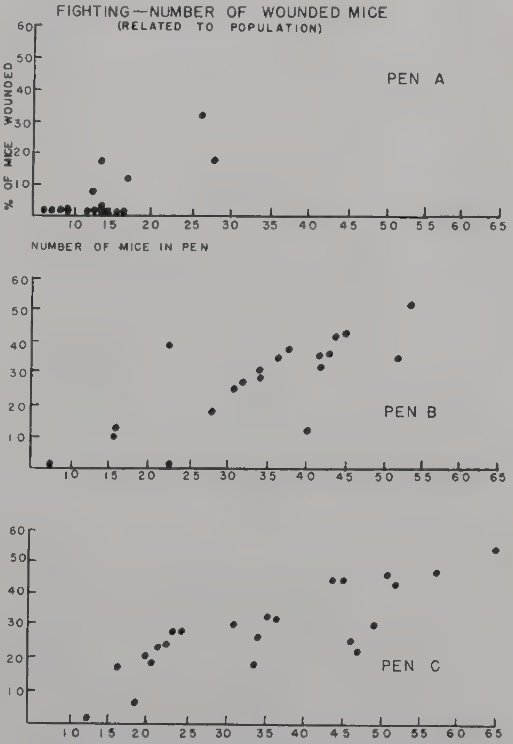

FIG. 4. Per cent of adult population wounded at the end of each month. Each dot represents the per cent of the adult population wounded at the end of a month.

to be found very soon after death in order to be of any use in finding evidences of disease, and for this reason relatively few autopsies were made. Only gross examination for pathological conditions was attempted and since accurate diagnosis requires histological and culture techniques only tentative diagnoses could be made.

The appearance of healthy and diseased animals was quite characteristic and resembled the description given by Worden (1947) for *Microtus agrestis*. The progress of disease was followed in a number of mice that were killed and autopsied shortly before they would have died anyway. Two sets of symptoms were observed that were very suggestive of mouse typhoid and infections arthritis as described by Snell (1941).

There was very little evidence of disease during most of the period of the study, diseased mice becoming common in the pens only during periods of population decline following very high population densities. Thus Table V shows that disease became very evident in Pens B and C during the period of population decline following the halving of the pen space. There was never a high incidence of disease in Pen A where the population never reached high densities.

TABLE V. Per cent of diseased animals in each population at the end of each month

Month	Pen A		Pen B		Pen C	
	Per cent diseased	Popul.* density	Per cent diseased	Popul.* density	Per cent diseased	Popul.* density
January	—	—	0.0%	0.06	0.0%	0.07
February	—	—	0.0	0.06	0.0	0.07
March	—	—	11.1	0.06	10.0	0.07
April	0.0%	0.05	12.5	0.05	0.0	0.09
May	0.0	0.05	0.0	0.09	0.0	0.09
June	0.0	0.10	3.7	0.18	0.0	0.11
July	0.0	0.13	3.2	0.20	0.0	0.13
August	0.0	0.13	6.5	0.20	0.0	0.15
September	7.6	0.09	12.5	0.21	9.1	0.22
October	0.0	0.09	0.0	0.25	2.5	0.15
November	0.0	0.19	9.0	0.30	0.0	0.23
December	0.0	0.17	2.7	0.25	0.0	0.33
January	0.0	0.05	0.0	0.23	0.0	0.35
February	0.0	0.04	0.0	0.23	0.0	0.33
March	0.0	0.04	2.0	0.34	5.9	0.34
April†	0.0	0.04	0.0	0.34	0.0	0.31
May	6.3	0.11	11.3	0.71	2.0	0.33
June	0.0	0.11	33.3	0.56	10.5	0.45
July‡	0.0	0.19	48.0	0.31	16.0	0.38
August	0.0	0.11	19.0	0.11	13.0	0.63
September	0.0	0.09	0.0	0.05	9.4	0.57
October	0.0	0.10	0.0	0.15	0.0	0.49
November	0.0	0.11	0.0	0.27	0.0	0.29
December	0.0	0.10	0.0	0.29	0.0	0.14

*Mice per square foot of pen space.
†Pen space in Pen B reduced by half.
‡Pen space in Pen C reduced in half.

Infectious disease has been considered by many writers to be an important factor in bringing about population declines in cyclic mammals. It may be reasonably assumed that as a population increases in density the chance of an epizootic occurring increases. Wayson (1927) described an epizootic among California meadow voles (*Microtus californicus*) in which the pathogenic organisms were those of mouse septicemia and swine erysipelas. Hamilton (1937) found manifestations of disease in high field mouse populations but no infectious organism. Findlay and Middleton (1934) found a Toxoplasma in declining populations of *Microtus agrestis* but it was found to play no part in bringing about the declines (Elton 1942). Chitty (1954) studied tuberculosis in populations of *Microtus agrestis* and concluded that the disease was not a major factor in bringing about declines. Green *et al.* (1938, 1940), in studying snowshoe hare declines, found a syndrome which they called "shock disease." The disease was found focally during times of low population density and took on epidemic proportions during periods of high population density. No pathogen was found.

It may be concluded that disease plays a part in bringing about population declines; but that it is the only factor, or even the major factor, has not been conclusively demonstrated. The results of the present study indicate that the animals of dense populations were more susceptible to disease than those of low populations. That this greater susceptibility may be related to changes in adrenocortical activity at high population levels is discussed in a following section.

ADRENOCORTICAL ACTIVITY

The number of circulating eosinophils was used as the criterion of adrenocortical activity, lower eosinophil levels indicating higher adrenocortical activity. Using the mean value for each of the 63 counting periods and the data from all the pens, the mean eosinophil count for population densities of under 30 mice per pen was 261.5 cells per cubic millimeter of blood and for over 30 mice per pen it was 129.7 cells per cubic millimeter of blood. The difference of 131.8 cells was significant at the 0.01 level of significance as indicated by t value of 6.074 with 61 degrees of freedom. This indicates that high population densities were accompanied by low blood eosinophil levels.

In Figure 5 the mean monthly eosinophil level is plotted against population density for each of the pens. The figure shows that high population densities were accompanied by low eosinophil levels. Table II shows that the coefficient of correlation between eosinophil levels and population density was negative for all of the pens and significant for pens B and C. Presumably the

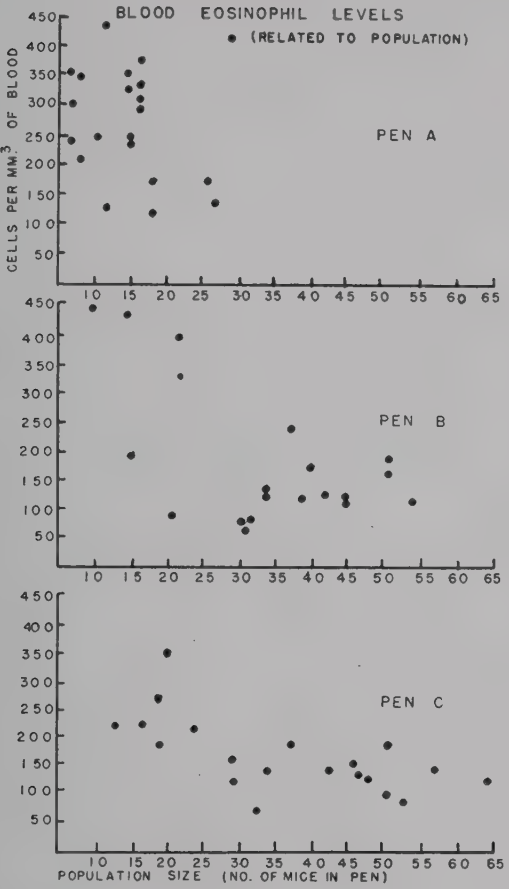

Fig. 5. Blood eosinophil levels plotted against population density. Each dot represents the mean eosinophil level for a given month.

population of Pen A never reached a high enough density to affect the eosinophil levels.

Additional evidence concerning adrenocortical activity at high population levels is afforded by the adrenal weight data obtained at the final autopsy terminating the study. At that time the population of Pen B was 42 mice, while that of Pen C was 20 mice and that of Pen A 15 mice. Only male adrenal weights were used since reproductive activity is accompanied by a marked increase in adrenal weight in the females. The mean male adrenal weight for Pen B was 0.144 milligrams per gram of body weight while that for Pen A was 0.104 milligrams per gram body weight and that for Pen C was 0.086 milligrams per gram of body weight. The difference between Pens B and A was 0.04 milligrams per gram of body weight which gave a *t* value of 2.500 which is significant at the 0.02 level of significance and 24 degrees of freedom. The difference of 0.058 between Pens B and C was significant at the 0.01 level of significance as indicated by a calcultated *t* of 3.222 at 23 degrees of freedom.

Adrenopituitary Activity, Behavior, and Demographic Factors

Fighting has been shown to be a stress factor bringing about increased adrenocortical activity. Clarke (1952) induced fighting in *Microtus agrestis* by introducing a strange vole into a cage containing a pair of resident voles. The fighting resulted in a pronounced increase in the weight of the adrenal glands and spleen, and a decrease in the weight of the thymus gland of the strange voles. The longer the period over which the fighting stress was applied the greater was the enlargement of the adrenals. Thus, a total of 20 hours fighting, when spread out over a period of nine to ten days, caused a greater adrenal enlargement than when given over a shorter period of time. Clarke suggests that the effect of fighting depends upon the length of time over which it is spread. Thus a vole may meet and fight another individual only once every 24 hours but if this is spread out over a long period of time it could amount to a considerable stress. In the present study, a condition could easily be visualized in a dense population where many of the animals would have some sort of fight, or interaction with another animal, every 24 hours if not more frequently. Since this fighting would be spread out over a considerable period of time it could well be an effective stressor.

Chitty (1952) suggested that intraspecific strife during times of high population density may have an adverse effect upon the hormonal balance of the females and thus bring about the production of less viable young. In this way he explained the high juvenile mortality observed at the time of the population peak, and the lack of reproduction in the breeding season following the peak.

Selye (1950) suggested that activities such as growth, reproduction, and lactation, not immediately necessary for the maintenance of life during an emergency, are inhibited because of a shift in the activity of the anterior pituitary gland towards the production of ACTH at the expense of the production of the gonadotrophic, growth, and lactogenic hormones. He gives evidence that exposure to stress brought about a reduced activity in the testes of male animals. The response of female rats to systemic stress was overian atrophy and more or less permanent anestrus.

Thus we have a possible mechanism whereby the stress of fighting, coupled with the inability of lactating females to isolate themselves from the disturbing influence of the population, would bring about decreased reproductive activity. In this study the actual rate of production of young did not change with increased population density, but the survival of litters decreased significantly.

Riddle *et al.* (1953) found that the administration of prolactin to virgin rats induced maternal behavior, and that prolactin was more effective after the rats were primed with FSH. They determined that, in rats, prolactin is responsible for the exhibition of maternal behavior such as retrieving of young and nursing. Prolactin has been found to stimulate parental behavior in fish, chickens and rats (Riddle and Bates 1939; Collias 1952). Thus it might theoretically be expected that inhibition of prolactin production by any factor will bring about a decreased maternal drive in the females and this will contribute towards higher litter mortality due to neglect or actual litter destruction on the part of the females. The stress factors of fighting and disturbance of lactating females, besides bringing about direct litter destruction, could produce a shift in the activity of the anterior pituitary inhibiting maternal drive and this could be contributory to the increased litter mortality observed at high population densities in this study.

According to Selye (1950), adaptation to one stressor in the Resistance Phase of the GAS is acquired at the expense of the ability to adapt to other stressors. Thus, in this study, a resistance may have been built up to the stress of fighting which accompanied high population levels. This resistance to the stress of fighting would have been acquired at the expense of resistance to other factors such as temperature changes, disease, the stress of handling, etc. That the animals of the high populations were more susceptible to infectious disease is evidenced by the fact that, although contagious diseases were endemic in all of the populations at all times, they reached epidemic proportions only following high population densities. Even when the populations in the pens were low the mice came into contact frequently enough to allow a contagious disease to spread if the animals had been susceptible.

Thus the manifest causes of population decline in the present study can be theoretically related to the response of the adrenopituitary system to the stressors accompanying high population density.

SUMMARY

The relationship between adrenopituitary activity and population density was studied in three confined populations of meadow voles in order to test Christian's (1950) hypothesis that high population density constitutes a stress factor which may limit population growth.

Three populations of meadow voles were introduced into enclosed pens and allowed to increase at their own rate. Changes in demographic, behavioral, and physiological phenomena accompanying increased population density were observed.

High population densities were accompanied by increased adrenocortical activity. The direct cause of this increased adrenocortical activity appeared to be the higher incidence of fighting that occurred in the pens during periods of high density. The demographic factors that appeared to limit population growth and bring about the population decline that followed high population densities were an increased litter mortality and adult mortality. The increased litter mortality was related to aberrant maternal behavior apparently brought about by disturbance of the lactating females due to their inability to isolate themselves from the rest of the population. The high adult mortality was brought about by an increased incidence of infectious disease at high population densities.

It is suggested that the animals of the high population were in the Resistance Phase of the General Adaptation Syndrome (GAS) in response to the stress factor of fighting and so were more susceptible to infectious disease which became an important mortality factor only at high population densities. A theoretical shift of anterior pituitary activity in the Resistance Phase of the GAS toward the production of ACTH and away from the production of the gonadotrophins and prolactin may partially explain the aberrant maternal behavior and thus part of the litter mortality observed at high population densities.

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ANNUAL CYCLE OF NET PLANKTON IN A FLUCTUATING NORTH-CENTRAL COLORADO RESERVOIR[1, 2]

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Introduction

Throughout the world there is an increased tempo in the construction of reservoirs. In most cases these are multipurpose water bodies. In some parts of the western United States the water areas have been greatly augmented by the building of dams for the storage of water. Although there have been many limnological studies in semi-arid regions of the west, there have been few investigations aimed at the determination of biological productivity in the sharply fluctuating "lakes." It is, therefore, the purpose of this paper to report the plankton quantity in a recently created north-

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[1] This paper is taken from a portion of a thesis submitted to the Graduate School at Colorado A & M College in partial fulfillment of the requirements for the degree of Master of Science.

[2] The authors wish to thank Dr. D. S. Rawson, Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan for reading the manuscript and offering many helpful suggestions.

central Colorado reservoir in which there is an extreme water fluctuation from season to season.

The reservoir considered in this study, known locally as Horsetooth Reservoir, is located four and one-half miles west of the city of Fort Collins, Larimer County, Colorado. The reservoir is approximately six and one-half miles long and one-half mile wide. When filled to capacity the "lake" has a maximum depth of 150 feet (46 m) and contains 146,000 acre-feet ($181 \times 10^6 m^3$) of water. The basins are partly natural and partly formed by excavation. The several earthen dams were constructed from soil and rocks removed from the previously existing valley which the lake now occupies. The substratum is composed of eroded clays, shales, and sandstone. Former water gaps in the sandstone formation help to account for the irregular shoreline (Fig. 1). These water gaps are now closed by dams. In general, the contour of the basin is sharply sloping. Because of the acute slope of the eastern and western shorelines, littoral zones are practically non-existent.

Construction of Horsetooth Reservoir was completed in 1949. By 1951 it was filled with water which had been diverted from the western slope of the Continental Divide. Since the reservoir is part of a project of the U. S. Bureau of Reclamation, water is collected from a variety of sources. For example, alpine water is mixed with both subalpine and montane run-off as the water passes through a complex of tunnels, siphons, natural streams, and temporary storage basins. In addition, precipitation runoff in the footholls area supplements the water sources mentioned above. All of this water is channeled into Horsetooth Reservoir by a main inlet at the south end of the lake, whereas water is released into canals at the north end of the lake. During late autumn and winter the amount of water entering the reservoir greatly exceeds the amount withdrawn, hence the maximum water storage occurs in the early spring. As irrigation demands for water are met the outflow exceeds the inflow and as a result minimum storage occurs in late summer.

The present investigation was carried on from October 1953, to September 1954. During this time physical, chemical, and biological factors were considered in an attempt to interpret the total net plankton productivity of the lake.

METHODS

Samples were taken at two week intervals by means of a ten-liter Juday plankton trap. Four stations on a transect from Spring Canyon Dam to the inlet were established. This allowed collections to be made in the area of maximum depth in the bay behind the dam (Sta. A), in the open area of the reservoir (Sta. B), in the inlet (Sta. D), and in the region of transition from inlet to the main reservoir (Sta. C) (Fig. 1). Water temperatures were taken by means of an electrical resistance thermometer.

Plankton collections were made in a vertical series at the surface, three feet, five feet, and ten feet at all stations. At Station A plankton was collected at the 20- and 35-foot levels and at 20-foot intervals thereafter. At Station B collections were made at the 25-foot level and at 20-foot intervals from there to the bottom of the lake. At Station C plankton collections were made at ten-foot intervals beginning at the ten foot level. At Station D collections were made at the 15- and 25-foot levels and at 15 foot intervals thereafter. These levels were used until the lowering water

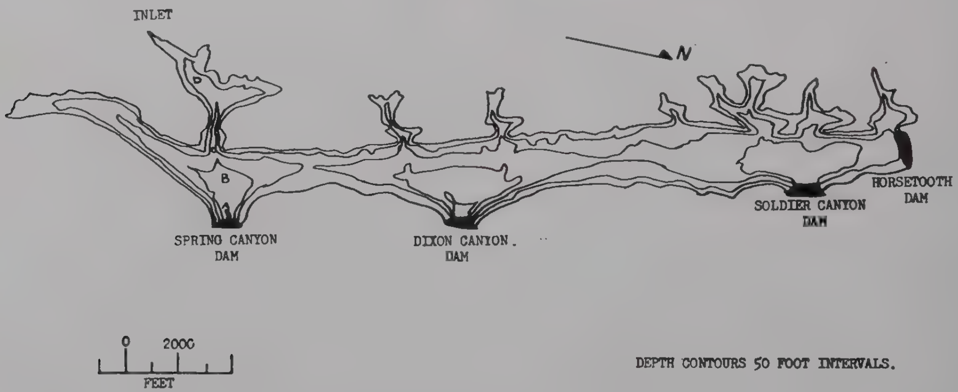

FIG. 1. Horsetooth Reservoir, Larimer County, Colorado. The sampling stations are located on a transect extending from the inlet to Spring Canyon Dam.

level made it impossible to secure samples from depths previously used.

A Sedgwick-Rafter chamber 50x20x1 mm with a capacity of one ml and ruled into four-mm squares, was used in counting plankton. Total counts of Rotatoria and Entomostraca were made on each sample. After total counts were completed the sample was diluted with six per cent formalin to a convenient volume for counting the remaining plankton. The most numerous organisms were counted in three squares taken at random and the number per cell computed. The less numerous plankters were counted in the entire aliqout. Two aliquots from each sample were counted. Counts of phytoplankton and Protozoa were made by cells. In such forms as *Asterionella* each cell was counted. In colonial forms, *Eudorina* for example, the average number of cells in several colonies was determined and this used as a factor. For filamentous algae the number of cells in a filament of known length (measured with an ocular micrometer) was determined and this used as a factor. Since the Sedgwick-Rafter chamber was graduated into four-mm squares, the number of cells per filament could be estimated by the length of the filament. The number of organisms per liter of lake water was taken to be equal to:

$$\frac{\text{number of organisms per counting cell x ml of concentrate x 1000}}{\text{number of liters of sample}}$$

For Rotatoria and Entomostraca the total count was divided by the number of liters in the sample to obtain the number of animals per liter of lake water.

On five occasions the dry weight of plankton per cubic meter of water was determined. Collections were made by the methods indicated above, and the combined catch at each station was evaporated to dryness and weighed.

Discussion

Horsetooth Reservoir with its irregular outline, multiple basins, and rather great depth is probably an atypical lake for north-central Colorado. Pennak's (1945a) description of 10 lakes, which he believed to be typical of the area, showed that these bodies of water are characterized by single basins, smooth shorelines and shallow depth. In another paper, this author (1941) stated that fluctuations of as much as four meters per year were exceptional, and that the usual size of north-central Colorado lakes is less than 50 acres. Thus Horsetooth Reservoir appears to be atypical also in its large area and in the magnitude of yearly fluctuation.

Both ends of the transect are protected from the prevailing southerly diurnal winds of summer (Fig. 1). However, such is not the case regarding northwest winds of autumn and winter. Waves generated as these winds sweep across the open lake pile water on the south shore of the bay. The course of this water is plainly marked by mud and silt as it flows obliquely along the shore and counter to the wind. The effect of wind on water temperatures in the bay region was pronounced. During the latter part of May 1954, a well defined thermocline occupied the 43-to-50-foot stratum, whereas in the first week in June the thermal stratification was destroyed by windstorms (Fig. 2). By late July the effect of circulation was even more pronounced. At this time the lowering water level exposed large areas of mud and silt that were previously deposited on the bottom. As a result of wave action, much of this material was resuspended. Although there was a tremendous amount of silt in the surface waters, there was little turbidity below the thermocline. This would indicate that the stratification was well established (Fig. 2), and that the denser water of the thermocline was an effective barrier against vertical circulation. This tends to confirm the observation of Ellis (1936) in which he reported that silt-laden waters, upon entering a lake, spread out along the surface of the cold hypolimnial waters. There were no profound changes in temperature until fall overturn. This occurred sometime in early September. Relatively homothermous conditions persisted throughout the winter months (Fig. 3).

In October 1953, the water depth at Station B in the center of the transect was 75 feet (23 m). As water was run into the reservoir the depth gradually increased to 150 feet (46 m) at the same station in April, thereafter water removed for irrigation purposes reduced the water level. In September the depth at Station B was reduced to 45 feet (14 m). During the course of this study, surface temperatures varied from 33° F to 72° F (0.5° C to 22.2° C), whereas the temperature just above the substratum ranged from 36° F to 44° F (2.2° C to 6.7° C) (Fig. 3). The lake was thermally stratified from mid-June to September.

The surface water was 80 per cent or more saturated with dissolved oxygen during nearly all of the investigation (Fig. 3). The maximum of 107 per cent of saturation in August accompanied a phytoplankton bloom which was composed of

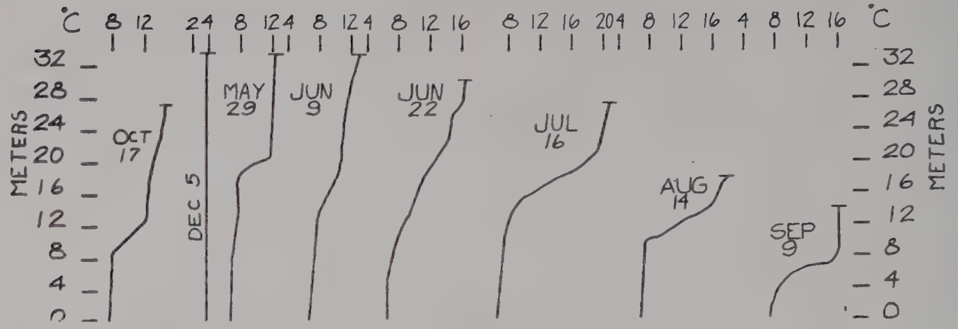

FIG. 2. Temperature curves for selected dates, Station B, Horsetooth Reservoir. The short bars denote water level (above bottom) on date of sample.

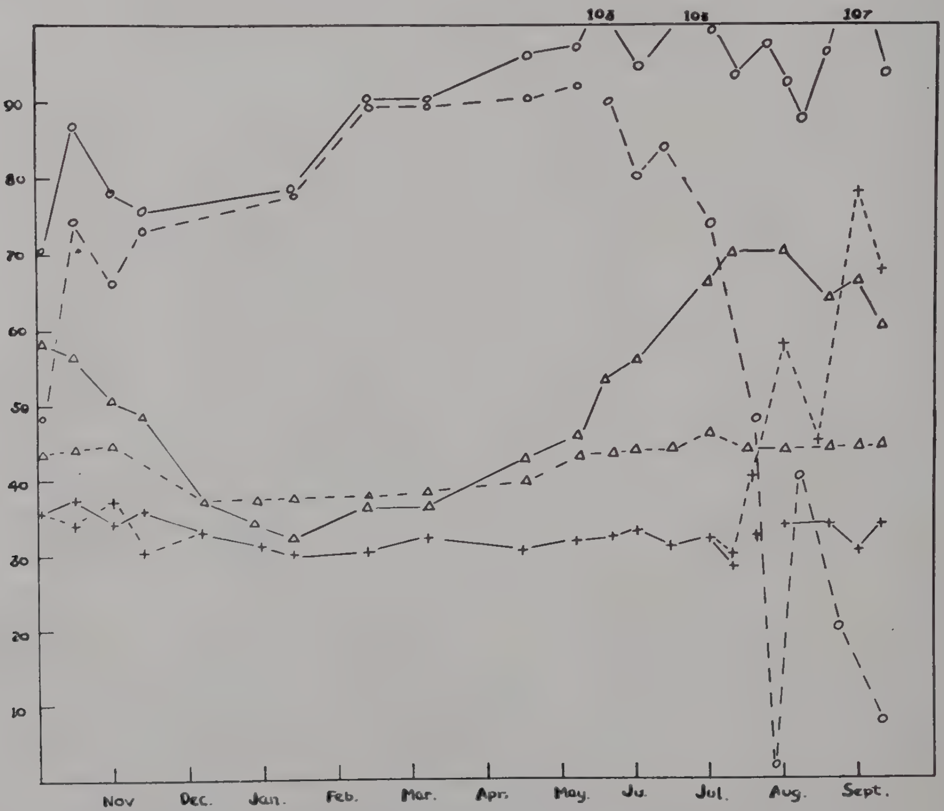

FIG. 3. Seasonal patterns of some chemical and physical factors in Horsetooth Reservoir as observed at Station B. The circles (O) represent dissolved oxygen in percentage of saturation, the triangles (Δ) temperature in degrees Fahrenheit, crosses (+) alkalinity in parts per million. The solid lines (———) indicate data from surface samples, the broken lines (------) show data from samples taken two feet above the substratum.

Eudorina, Binuclearia, and *Asterionella.* Thermal stratification was followed by reduction of dissolved oxygen in the hypolimnion.

The alkalinity of Horsetooth Reservoir is due to bicarbonates. The HCO_3^- concentration in the surface water remained fairly uniform throughout the study (Fig. 3). Bicarbonates reached a peak of 78 ppm as a result of accumulation in deep water during summer stagnation. The hydrogen ion concentration of the hypolimnion was slightly acidic 6.5. The pH of the surface water ranged between 7.3 and 7.5.

The phytoplankton exhibited vernal and autumnal maxima. The vernal pulse was composed of Bacillariacae and Chlorophyceae dominated by the diatoms *Asterionella, Fragilaria,* and the colonial flagellate *Eudorina.* The diatom *Asterionella* and the chlorophyceans *Eudorina* and *Binuclearia* constituted the autumnal bloom (Fig. 4).

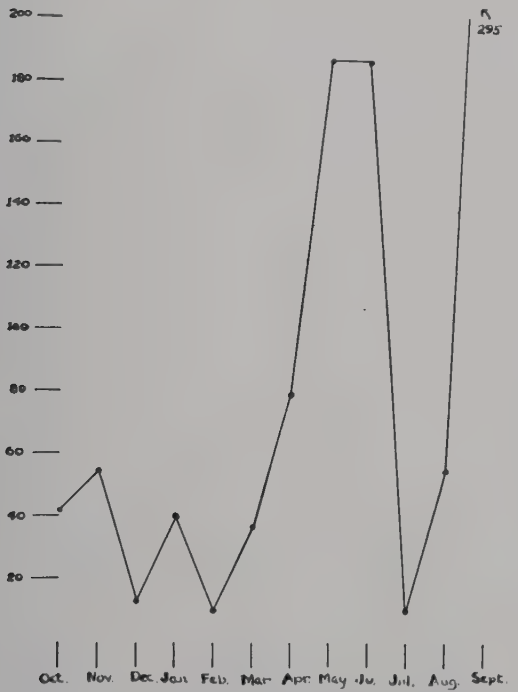

FIG. 4. Annual variation of phytoplankton expressed in millions of cells per liter (average of all samples from four stations).

Zooplankton numbers fluctuated markedly. Numerically the Protozoa were prominent (Fig. 5), whereas the Crustacea and Rotatoria were inconspicuous (Fig. 6). Unfortunately it was not posisible to differentiate seasonal successions from effects that fluctuating water level may have had on the numbers of phyto- or zooplankters.

Total solids averaged 42 miligrams per liter in Horsetooth Reservoir. In most cases, higher total-solid values coincided with low Secchi-disc readings and phytoplankton pulses, indicating that material in suspension rather than true solutes made up the greater portion of total solids. Pennak (1949) in an investigation of seven northern Colorado reservoir lakes found that dissolved solids varied from 36.3 to 5,480.4 milligrams per liter, and only one lake contained less than 100 miligrams per liter. Thus it appears that Horsetooth Reservoir is atypical in dissolved solids when compared to other lakes of the region. Pennak (1949) found that the maximum and minimum amounts of dissolved solids were associated with the most and least productive reservoirs, respectively. Moyle (1946) believed that Minnesota lakes with less than 40 ppm total alkalinity were apt to be of low productivity.

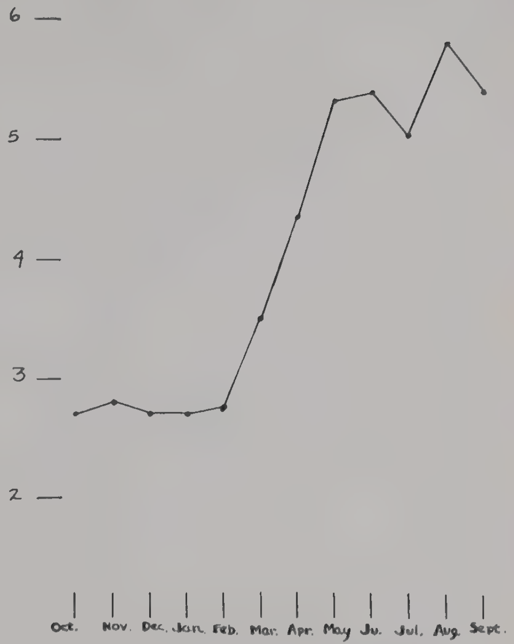

FIG. 5. Protozoa expressed as the logarithm of number of cells per liter (average of four stations).

Pennak (1945b) pointed out that the rocks of the Continental Divide area are relatively insoluble. He also called attention to the importance of length of time in which water has been in contact with the substratum. When one considers the alpine and subalpine sources of water entering Horsetooth and the rather short time that the water is in contact with the sandstones that form the reservoir basin, it is not surprising to find small amounts of dissolved solids.

The dry weight of plankton varied from 110.0 to 512.6 mg per cubic meter of water and averaged 262.0 mg (Fig. 7). The dry weight of plankton per hectare ranged from 20.6 kg to 78.0 kg, with 43.5 the average (Fig. 8). The above values are, of course, measures of the standing crop of net

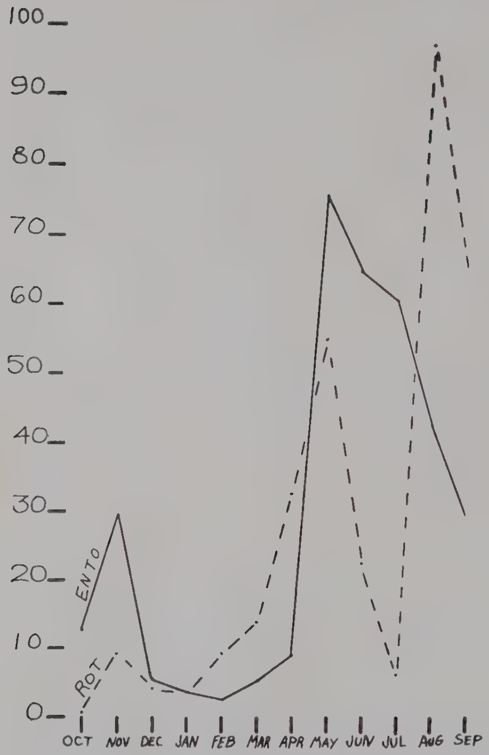

FIG. 6. Entomostraca and Rotatoria, number of organisms per liter, Station B.

plankton at the time of sampling and as such are subject to certain shortcomings as pointed out by Clark (1946). However, Rawson (1939, 1953a) has indicated that the inverse relationship of standing crop of plankton to mean depth is valuable in estimating productivity.

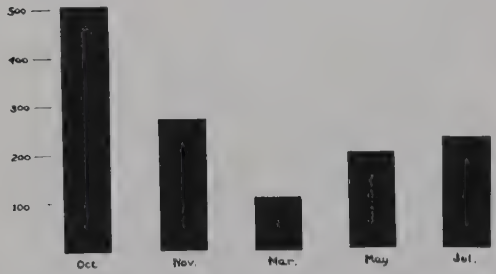

FIG. 7. Net plankton expressed in milligrams of dry weight per cubic meter of water.

Ruttner (1953) has indicated the advantages of expressing productivity in terms of weight per volume.

For any given volume, surface is a function of depth. Hence, dry weight of plankton per volume from a vertically spaced series of samples, when converted to weight per unit of surface, should in theory yield a good measure of the standing crop of a given basin type. As mentioned above, the average dry weight of net plankton in Horsetooth Reservoir was 43.5 kg/ha or 38.2 lb/acre. Juday (1940) reported the average dry weight of Lake Mendota centrifuge plankton to be 240.0 kg/ha. Rawson (1953b) reported 6.8 kg/ha net plankton for Amethyst, a strongly oligotrophic alpine lake in Alberta, Canada. He also suggested 50 kg/ha as the approximate lower limit of net plankton for mesotrophic lakes. Perhaps on the basis of dry weight of plankton per surface unit Horsetooth Reservoir could be considered a mesotrophic lake.

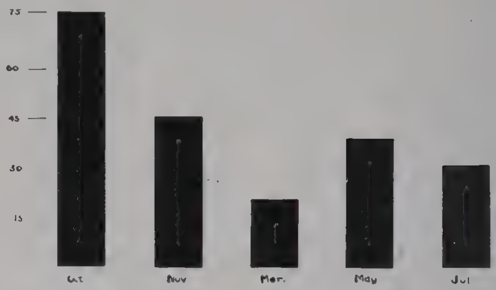

FIG. 8. Net plankton expressed as kilograms dry weight per hectare.

After working with the plankton of Lake Mendota for many years, Birge (1922) concluded that the dry weight was about one-tenth of the wet or live weight for plankton. Juday (1940), after much experience with Mendota plankton, estimated the average rate of turnover throughout the year to be once each two weeks.

If one accepts both the figures given by Birge for the ratio of dry weight to wet weight, and Juday's concept of rate of turnover of plankton, some insight into the total net plankton produced within Horsetooth Reservoir in a year's time may be gained. Ten times 38.2 (the average dry weight in lb/acre) gives an average of 382 pounds of living plankton per acre of lake surface. This multiplied by 62 (bi-weekly rate of turnover) equals 9,932 pounds or nearly five tons of plankton produced per acre. If the average surface was 1,300 acres, then total plankton production for the year was 12,911,000 pounds or approximately 6,455 tons.

SUMMARY

1. A limnological investigation of the annual standing crop of net plankton in a fluctuating reservoir was conducted from October 1953 to Sep-

tember 1954 on Horsetooth Reservoir in north-central Colorado.

2. Chemical, physical, and biological samples were taken at two-week intervals. Plankton was obtained by means of a 10-liter Juday trap.

3. The water level fluctuated markedly from a maximum depth of 150 feet (46 meters) in April to a minimum depth of 45 feet (14 meters).

4. Horsetooth Reservoir produced an average dry weight of plankton of 32.2 pounds per acre and may be considered mestotrophic in nature.

5. Total net plankton production for the year was estimated to be of the order of 6,000 tons.

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POPULATION DENSITY OF THE LIMNETIC CLADOCERA OF PYMATUNING RESERVOIR[1]

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INTRODUCTION

The interrelationships between a population and its natural environment are best inferred from a study of a sample of the population in this natural environment. To obtain the broadest possible basis for inference, samples of organisms should be studied from several different natural environments where both the responses of the organisms and the chemical, biological, and physical factors of the environment can be quantitatively measured. The virtual impossibility of actually controlling variability in the field makes difficult the determination of the nature and extent of the influence exerted upon the organisms by any environmental factor or combination of factors. The application of various statistical methods to the data does, however, enable the investigator to measure, partition, and evaluate the variance in data collected from the uncontrolled natural environment. It was the purpose of this investigation to determine from quantitative measurements made in the field the effect of certain environmental factors on the density of a population of limnetic Cladocera.

Pymatuning Reservoir, a highly productive eutrophic lake constructed in 1934 on the Pennsylvania-Ohio border about 40 miles south of Lake Erie, is the site of this investigation. This lake has been previously studied by Tryon and Jackson (1952); on the basis of their chemical, biological, and physical findings the three subdivisions of Pymatuning (designated in Figure 1 as Sanctuary, Middle, and Lower lakes) can be considered as three ecologically distinct lakes.

Cladocera were selected as the subjects for the present study for two reasons. The high reproductive capacity of these animals enables them to quickly respond to and utilize favorable environmental conditions. Secondly, the high numbers of Cladocera found in Pymatuning (Table I) constitute evidence of an unique situation and should facilitate a study of the ecology of these animals.

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[1] Pymatuning Laboratory Publication No. 14. This material was originally presented as portions of a doctoral dissertation at the University of Pittsburgh in 1954 under the direction of C. A. Tryon, Jr. The work was in part supported by a National Science Foundation Fellowship. Author's present address: 135 Fieldstone Ave., Johnstown, Pennsylvania.

METHODS

This investigation covered a period from June, 1952 to September, 1953. Sampling was designed to include three weekly samples of the water and the organisms at each of two stations from each of the three lakes (Fig. 1) for the months of May through September. Biweekly samples for the remaining months were taken as weather permitted.

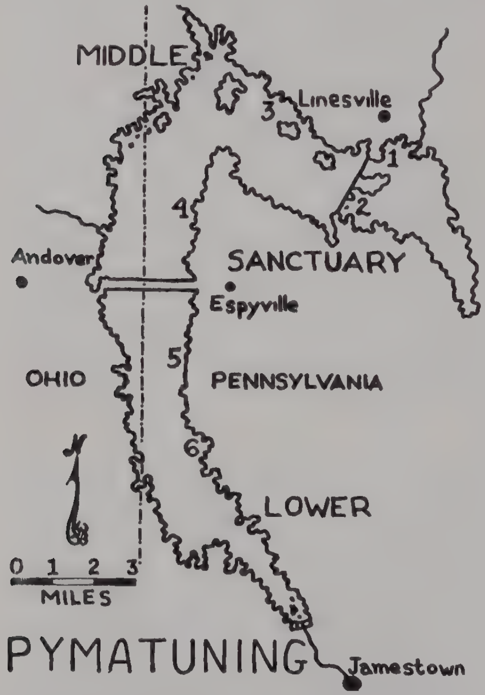

FIG. 1. An outline map of Pymatuning Reservoir showing the three lakes—Sanctuary, Middle, and Lower—of which it is composed and the location of the six sampling stations.

Water samples were made with a Foerst water sampler. One liter of water was poured through a Kofoid plankton bucket covered with number 17 silk bolting cloth and the concentrated sample was preserved with a few milliliters of alcohol. Each concentrated sample was evenly dispersed over a large glass counting chamber ruled off into 49 squares, each one centimeter on a side. The total number of Cladocera in each liter sample was then estimated by counting the numbers of Cladocera in each of seven randomly selected squares and then multiplying by seven. The results of this sampling are summarized in Table I. The genera and species were identified from keys in Ward and Whipple (1918) and Pennak (1953). The author is indebted to Dr. John L. Brooks of Yale University for the identification of the Daphnia. The percentage composition of the Cladocera population based upon the numbers of each genus per liter as well as the monthly average total numbers of Cladocera per liter at each of the six stations is shown in Figure 2.

For each water sample the following chemical measurements were made immediately in the field:

(1) Oxygen, by the unmodified Winkler method, in ppm.

(2) Phenolphthalein and methyl orange alkalinity in ppm.

(3) Total acidity in ppm.

(4) Hydrogen ion concentration using, during 1952, a Hellige colorimetric pH meter and, during 1953, a Beckman pH meter. These analyses were run according to the methods in Standard Methods (Amer. Pub. Health Assoc., 1946). Air and water temperatures were measured with a centigrade thermometer. Table I summarizes the results of the chemical analyses for each of the six stations.

During the summer of 1953 samples of bottom materials from the three lakes were dried, ashed, and weighed for estimates of their organic content as described in Welch (1948). During this same period at each station an additional liter of water was collected, concentrated in a Foerst electric centrifuge, dried, ashed, and weighed (Welch 1948) for an estimate of the particulate organic matter in the water. Table II shows the mean per cent of organic matter in the bottom soils and the mean milligrams of particulate organic matter per liter of water in each of the three lakes based on these samples.

ANALYSIS OF CHEMICAL DATA

Pymatuning is, primarily, an alkaline lake. The total range of pH values was from 6.2 to 10.3 corresponding to a hydrogen ion concentration of 6.31×10^{-7} to 5.01×10^{-11}. The values of carbonate ion expressed as parts per million of calcium carbonate varied from 0 to about 30, which, according to Welch (1952) classifies Pymatuning as a medium-water lake. As seen from Table I, the bicarbonate alkalinity was highest in Sanctuary lake (up to 52 ppm). On ten occasions samples were taken in which there was no bicarbonate alkalinity. At these times the algal bloom on the lake was heaviest. Total acidity, given in parts per million of acidity expressed as calcium carbonate, varied from 0 to about 36. It was taken as a measure of the free

TABLE I. The mean, standard deviation, and number of samples taken at each station for: pH; ppm of oxygen, bicarbonates, carbon dioxide, and carbonates; numbers of each genus and total numbers of Cladocera per liter

Lake......		SANCTUARY		MIDDLE		LOWER	
Station...... No. of Observ.......		1 44	2 45	3 40	4 40	5 40	6 40
Oxygen	m	8.9	8.6	9.0	9.3	9.9	8.6
	sd	2.46	2.09	2.59	2.22	1.88	1.52
Hydrogen Ion	m	6.31×10^{-9}	1.00×10^{-8}	6.31×10^{-9}	3.98×10^{-9}	6.31×10^{-9}	6.31×10^{-9}
	sd	.87	.87	.99	1.00	.91	.88
Bicarbonate	m	37.0	38.6	25.8	23.0	25.0	25.5
	sd	10.9	10.7	33.8	12.0	11.1	11.1
Carbon Dioxide	m	3.0	3.8	3.8	2.2	2.9	2.7
	sd	5.21	5.19	6.28	3.61	4.49	4.60
Carbonate	m	8.9	6.6	7.5	8.7	6.2	6.4
	sd	12.8	12.5	9.4	10.0	7.6	8.9
Bosmina	m	210.37	159.82	75.06	57.83	26.53	48.12
	sd	346.83	442.44	213.53	173.69	90.19	171.38
Ceriodaphnia	m	60.36	21.10	0.66	0.32	0.00	0.27
	sd	116.33	53.11	1.73	0.99	0.00	1.11
Chydorus	m	303.50	537.35	99.87	70.11	30.77	15.90
	sd	378.06	639.90	113.13	78.22	55.79	18.64
Daphnia	m	52.28	48.86	23.81	8.92	6.25	6.03
	sd	91.15	90.55	35.77	12.30	23.15	15.35
Diaphanosoma	m	15.83	16.41	5.79	3.22	2.29	1.41
	sd	33.97	47.06	11.31	6.45	5.35	3.70
Total Numbers	m	641.54	787.42	36.96	147.28	65.81	72.70
	sd	691.54	806.41	204.40	175.60	113.77	172.73

TABLE II. A comparison of Sanctuary, Middle, and Lower lakes with respect to depth, density of Cladocera, and organic matter in their waters and bottom soils. Mean values and standard deviations are given

Lake	Mean Depth in Meters		Number of Cladocera per Liter Water	Milligrams Organic Matter per Liter	% Organic Matter in Bottom Soils
Sanctuary..	1.5	m	872.9	18.2	45.64
		sd	865.76	3.90	24.60
Middle....	5.5	m	205.7	13.4	23.63
		sd	249.57	3.81	25.55
Lower.....	6.7	m	92.4	9.7	11.64
		sd	186.44	3.92	3.89

carbon dioxide since no acidity from mineral acids was detected using methyl orange as an indicator (Ellis, Westfall, and Ellis 1948). Oxygen varied from five parts per million (36% saturation) in winter or early spring to about fourteen parts per million (170% saturation) in summer. The oxygen content of the lake was usually from 90 to 100% saturation, due in part to the photosynthetic action of the dense algal population and in part to the influence of the wind upon water movements in a body of water as shallow as Pymatuning. Table II shows the mean depth of each lake.

Analysis of variance of chemical data between lakes and years was made and the results of this analysis are summarized in Table III. The lakes differ significantly only in their amounts of bicarbonate ion.

ANALYSIS OF THE BIOLOGICAL DATA

From Table I it can be seen that the numbers of Cladocera in Pymatuning are an outstanding characteristic. Five species of Cladocera occurred in the plankton of Pymatuning in such numbers and with such regularity that an analysis of their relationship to the environment seemed possible. These species were: *Bosmina longirostris, Ceriodaphnia reticulata, Chydorus sphaericus, Daphnia galeata mendotae,* and *Diaphanosoma brachyurum.*

In most lakes the numbers of Cladocera are reported to be from 0 to about 70 per liter (Juday 1915; Hutchinson and Pickford 1932; Coker and Hayes 1940; Tressler, Wagner, and Bere 1940). Pennak (1949) reports a Bosmina pulse of 397 animals per liter; Cheatum, Longenecker, and Metler (1942) found 66 Daphnia per liter in September and 60 in July, while finding a maximum of 40 Bosmina per liter. Ward (1940), re-

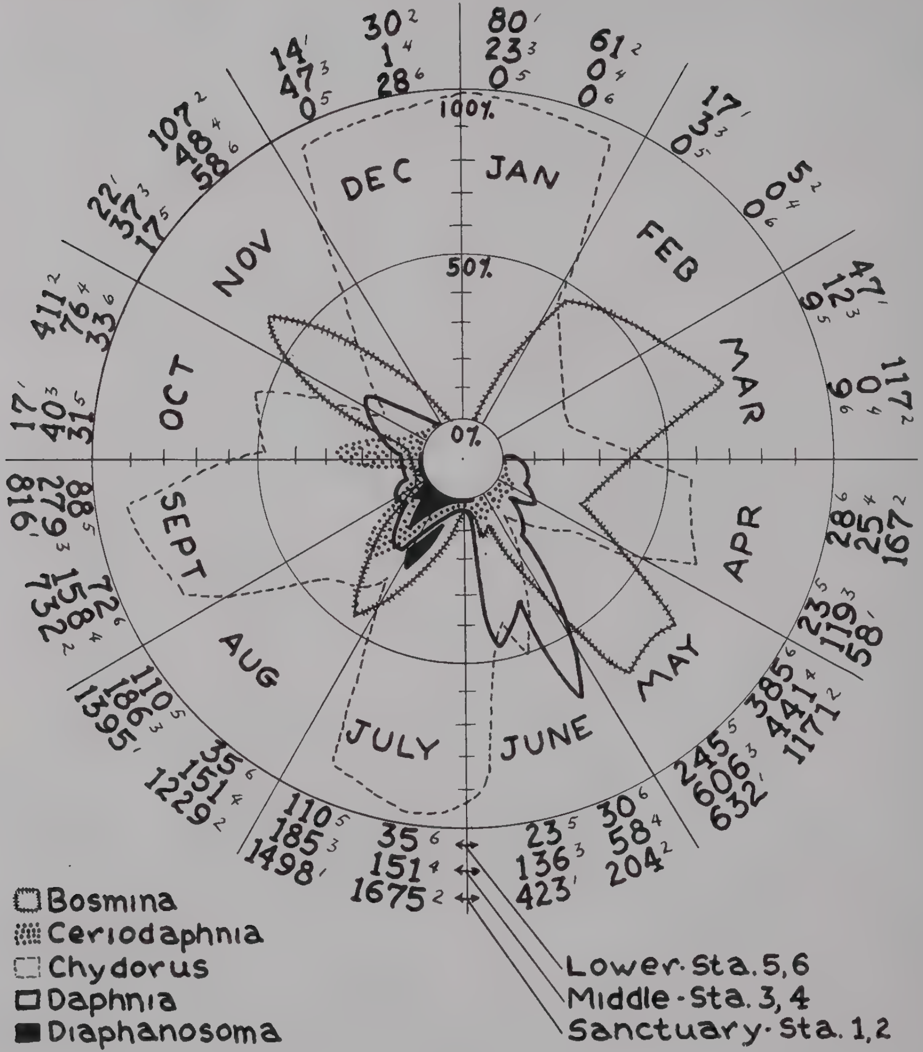

Fig. 2

cording as many as 2000 Cladocera per liter in a small pond in the spring and 800 per liter in July, found that temperatures induced the seasonal fluctuations and got little or no correlation between numbers and any other environmental factor.

For station one in Pymatuning the total numbers of Cladocera per liter ranged from 6 in April to 3547 in July; at station two, 2746 in May and 2891 in August. Maximum numbers at station three were 1290 per liter in May; for station four, 893 in May; for station five, 569 and for station six, 975 in May. Each genus reached its maximum during certain months (Ward 1940; Smyly 1952). Bosmina in Pymatuning reached their highest numbers (1000 or more per liter) in the middle of May with a second smaller peak about mid-July. Ceriodaphnia were practically absent until July when their numbers began to increase toward an August maximum of several hundred per liter. Chydorus were present in substantial numbers throughout the year, but reached their maximum in July and August when they numbered as high as several thousand per liter. Daphnia were comparatively regular in occurrence reaching maxima of several hundred per liter in

Table III. Analysis of variance showing the degrees of freedom and mean squares for concentrations of chemical factors and density of Cladocera associated with lakes, years, and error. Mean squares significant at the 5 and 1% levels are marked with a single or double asterisk

Source of Variation	Degrees Freedom	Variates				
		Oxygen	pH	Bicarbonate	Carbon Dioxide	Carbonate
Lakes	2	5.02	.93	4,831.51**	222.73	72.31
Years	1	74.28**	.49	778.56**	74.66	530.40*
Error	242	4.36	.85	120.47	216.19	108.58

		Bosmina	Ceriodaphnia	Chydorus	Daphnia	Diaphanosoma	Total Number
Lakes	2	521,256.83**	46,216.02**	3,940,752.92**	46,266.29**	4,989.42**	10,273,905.73**
Years	1	148,108.08**	8,740.80	210,591.01	9,974.66	720.99	879,211.21*
Error	242	69,207.10	2,866.66	102,953.90	3,315.29	638.77	219,658.38

June and again in late August or early September. Diaphanosoma, like Ceriodaphnia, were scarce until July when from one to two hundred animals per liter could be taken. Figure 2 shows what proportion of the total numbers of Cladocera per liter each genus represented throughout the year. The total numbers of Cladocera showed two peaks: one in May, the other in July. These two peaks were composed mostly of Bosmina and Chydorus.

An analysis of variance was applied to the numbers of each genus per liter and to the total numbers of Cladocera per liter associated with lakes and with years. Table III summarizes this analysis. It will be noted that the lakes varied significantly with respect to the total numbers of Cladocera per liter. The correlation coefficients between numbers per liter and the chemical factors are summarized in Table IV. The three positive correlations between total numbers and oxygen, bicarbonates, and carbonates are noteworthy in view of subsequent analyses.

Table IV. The coefficients of correlation between Cladocera densities and concentrations of chemical factors. Single and double asterisks indicate significance at the 5 and 1% levels

	Bosmina	Ceriodaphnia	Chydorus	Daphnia	Diaphanosoma	Total Number
Oxygen	−.0231	.0488	.0488	.0559	−.0831	.1689**
pH	−.1608*	.1718**	.2395**	−.0683	.1382*	.0904
Bicarbonate	.1033	.0930	.1289	.2493**	.0413	.1754**
Carbon Dioxide	.0687	−.0684	−.0381	−.0497	−.1003	−.0970
Carbonate	.0794	.2476**	.2397**	−.0470	.1704**	.2922**

An analysis of variance between numbers of animals associated with different concentrations of certain of the chemical factors was performed. The chemical factors chosen were oxygen, pH, and bicarbonates, since some measurable amount of each of these was, with very few exceptions, always present. To make this analysis, the total range of values for each factor was divided into three parts. For bicarbonates the three parts were: 0-17 ppm, 18-35 ppm, and 36-53 ppm; for oxygen: 5.0-7.9 ppm, 8.0-10-9 ppm, and 11.0-13.9 ppm; for pH: pH 6.2-7.5, pH 7.6-8.9, pH 9.0-10.3. Three groups were delimited because this provided at least two degrees of freedom which facilitated statistical analysis of the data. The number of groups was not increased because with only three the range of values with each group was wide enough to include concentrations the effects of which might possibly differ from the effects of concentrations in the other groups. The three groups of each chemical factor might therefore be considered as three different treatments.

The results of this analysis are shown in Table V. The different levels of oxygen concentrations had no significant influence on the Cladocera density, a result in keeping with the fact that most of the oxygen values recorded were near the saturation value. Though the total numbers of animals per liter did not differ with respect to pH, the densities of the component genera did, while both densities of total numbers and certain of the genera differed significantly with respect to the three levels of bicarbonate concentration.

Finally the methods of multiple regression and covariance were applied to the data. The densities of Cladocera were regressed on the following pairs of chemical factors: pH-carbonates; bicarbonates-oxygen; carbonates-oxygen; bicarbonates-

TABLE V. Analysis of variance showing degrees of freedom and mean squares for Cladocera densities associated with the various concentrations of oxygen, hydrogen ion, and bicarbonate ion. Mean squares significant at the 5 and 1% levels are indicated

Source of Variation	Degrees of Freedom	VARIATES					
		Bosmina	Ceriodaphnia	Chydorus	Daphnia	Diaphanosoma	Total Number
Oxygen	2	15,020.89	1,862.80	19,103.85	3,726.09	762.17	245,023.43
Error	240	69,658.65	2,890.55	103,652.65	3,311.86	637.51	219,443.00
Hydrogen ion	2	330,693.26*	12,853.84*	1,625,714.35**	17,410.84	901.97	286,409.49
Error	240	67,253.06	2,798.96	90,264.22	3,197.82	636.58	219,103.38
Bicarbonate	2	101,934.06	2,537.06	648,185.74**	36,079.15**	2,413.36*	1,818,698.09**
Error	240	68,934.38	2,884.93	98,410.30	3,442.25	623.98	206,333.04

pH; bicarbonates-carbon dioxide; and carbonates-bicarbonates. In these first six tests only the sums of squares and products associated with lakes and with years were subtracted from the total sum of squares to get the sum of squares associated with error. (Table VI shows one of the analyses of multiple regression and covariance in which the variation from an additional source—pH levels—is accounted for.) The lakes and error sums of squares and products were then used in a regression with the above-listed pairs of chemical factors. This regression, in effect, adjusted the variability among densities of Cladocera to what it would be if each lake had identical concentrations of the two chemical factors. The diffrences between lakes in numbers of Cladocera per liter still remained significant. The sum of squares for densities was greatly reduced by regression of

TABLE VI. A multiple regression and covariance analysis showing the sources of variation accounted for, their degrees of freedom, and their associated sums of squares (e.g., row N x column N) and of products (e.g., row B x column C). The mean squares for lakes and error, their F ratios, and the F ratios at the 1 and 5% levels of significance for the appropriate degrees of freedom both before and after regression are given for comparison

Source of Variation	Degrees Freedom	Variate	SUMS OF SQUARES AND PRODUCTS		
			No./Liter (N)	Bicarbonate (B)	Carbonate (C)
Total	248	N	75 123 787.09	299 249.04	416 863.18
Stations	5	..	21 087 249.03	444 538.71	11 781.11
Years	1	..	879 211.21	26 163.25	21 594.92
pH Levels	2	..	572 816.99	−117 879.77	97 075.99
Lakes	2	..	20 547 811.47	436 368.78	25 897.10
Error	240	..	52 584 509.86	− 53 573.15	286 411.16
Total	...	B	....	39 802.25	− 23 276.28
Stations	...	..	....	9 875.66	202.91
Years	...	..	....	778.56	642.61
pH Levels	...	..	....	24 490.67	− 19 481.02
Lakes	...	..	....	9 663.01	339.41
Error	...	..	....	4 662.36	− 4 641.78
Total	...	C	....	....	27 089.11
Stations	...	..	....	....	282.51
Years	...	..	....	....	530.40
pH Levels	...	..	....	....	17 511.73
Lakes	...	..	....	....	144.61
Error	...	..	....	....	8 764.41

Analysis of Variance

Source of Variation	D. F.	Sum of Squares	Mean Square	R^2	ERRORS OF ESTIMATE		
					Sum of Squares	d. f.	Mean Square
Lakes plus Error	242	73,132,321.33	....	.4673	38,957,587.57	240	....
Error	240	52,584,509.86	219,102.12	.2601	38,907,278.85	238	163,475.96
Lakes	2	20,547,811.47	10,273,905.74	.....	50,308.72	2	25,154.36
		$F=46.9^{**}$ ($F_{.01}=4.71$)			$F=6.49$ N.S. ($F_{.05}=19.49$)		

densities upon parts per million of bicarbonates and carbonates. In this analysis the *F* ratio (Snedecor 1946) between the mean square for lakes and the mean square for error—df 2/240—was reduced from 46.77 before regression to 5.39 after regression. The *F* ratio 5.39, although still significant, is approaching a non-significant level.

In an analysis of variance when the sum of squares for carbonates associated with the three different levels of pH was subtracted from the total sum of squares for carbonates, the consequent reduction in the error sum of squares rendered significant the sum of squares for lakes. Therefore when freed from the effects of varying concentrations of hydrogen ion, the concentrations of carbonate ion differed significantly between the three lakes. Although lakes do not differ significantly with respect to pH, the pH is highly variable and this variability could obscure any differences between lakes for any factor which is correlated with pH. Carbonates and pH are correlated and when the uncontrolled variability because of pH is removed, the carbonate concentrations become significantly different between lakes. To check this result, the carbonate sums of squares for lakes and error were regressed on pH. This operation statistically removed the effects of pH variability from the carbonate variability in a way different from the way in which this is achieved in analysis of variance. The result of regression was the same: the carbonate sum of squares associated with lakes attained the level of significance.

In accordance with this finding, the sums of squares and products for numbers, carbonates, and bicarbonates associated with the three levels of pH were subtracted from their respective total sums of squares and products. The sums of squares and products for lakes and for years were also subtracted from the total as before. The resultant sum of squares for error—that is, the unassignable variation—was thereby reduced and the test was refined. When these sums of squares and products for Cladoceran densities associated with lakes and with error were regressed on the concentrations of carbonates and bicarbonates, the errors of estimate for lakes were so decreased that the mean square, in comparison with the mean square for error, was not significant. Three other analyses were made in which the variation associated with pH and oxygen levels was removed and the remaining sums of squares and products for densities and such chemical factors as bicarbonates, carbonates, carbon dioxide, and pH were used in regression. None of these combinations of factors reduced the lake errors of estimate below the significant level.

DISCUSSION

The three component lakes of Pymatuning differed significantly in the densities of their limnetic Cladocera populations, which means that for the density-independent factors which affect Cladocera numbers these three lakes may differ. One way of finding which factors or combination of factors influence these organisms would be to control the variability of selected factors. Actual physical control of the factors in a natural environment is not feasible since, even if it were possible, the fact that variability would be artificially controlled would make the environment no longer a natural one. With multiple regression and covariance the effects of variability in environmental factors—factors with which the reactions of an organism are correlated—can be removed from the total variability of that organism's responses. Thus the effect upon the organism of any one factor independent of one or several other factors not only can be determined, but also the effect upon the organism of an environment in which the several factors remain constant. If to each of several environments populations of the same organisms react differently, and if between these several environments differences in their factors can be demonstrated, the effect of these differences can be statistically controlled and the consequent reduction of the environments to a common level for each of those factors is thereby effected. When the environmental factors selected for statistical control are ones which influence the distribution and densities of organisms, then any difference between the reactions of the organisms to these environments should be decreased as the differences between the environments are decreased.

If the factors influencing Cladocera densities in Pymatuning are found and the variation between lakes in Cladocera densities due to the variation between lakes in these factors is removed, then the remaining variation between lakes in densities should be no more than the usual variation found in sampling from a single uniformly distributed population. To test this hypothesis the methods of multiple regression and covariance were applied to the data on Cladocera densities and to the data on the concentrations of various chemical factors from the three lakes that constitute Pymatuning Reservoir.

In the analysis shown in Table VI, that portion of the variance which could be attributed to variation in hydrogen ion concentration was removed from the total variability of each variate. In a multiple regression that variability in densities of Cladocera which could be attributed to variation in amounts of carbonate and bicarbonate alkalinity was removed. The mean square of the errors of estimate for lakes, representing that variability between lakes in densities which could not be explained by regression, was compared with the mean square of the errors of estimate for experimental error. After regression the errors of estimate for experimental error were an estimate of the uncontrolled variation in densities freed from the effects of variation between lakes, years, and hydrogen ion concentration and independent of variation in bicarbonate and carbonate ion concentration. It is then an estimate of the variation found in sampling from a single uniformly distributed population under the conditions of this investigation. As a result of this analysis the mean square for the errors of estimate for lakes did not significantly differ from the mean square for experimental error. Therefore when the lakes were statistically adjusted to a common carbonate, bicarbonate, and hydrogen ion concentration their densities of Cladocera were no longer significantly different.

These results might be interpreted in two ways. The most direct conclusion would be that the numbers of Cladocera are dependent upon the concentrations of the three chemical factors: hydrogen ion, carbonate ion, and bicarbonate ion. This is not, however, in agreement with the findings of other investigators who, in studying lakes with similar concentrations of these factors, found no comparable numbers of Cladocera and no correlations between numbers of Cladocera and the chemical factors. The possibility exists that only in an environment supporting such high densities of Cladocera could these relationships be determined.

In the second possible way of interpretation these three chemical factors are not in themselves considered to be factors that determine the density of Cladocera in the natural environment. They are, instead, interpreted as indexes of the photosynthetic activity of the lakes which activity is, in turn, considered to have a direct influence upon Cladocera densities.

Most of the fluctuation in pH in the lakes can be attributed to this photosynthetic activity. Upon the different basic amounts of carbonate found in each lake are built the variations in concentration caused by photosynthesis. Since only the recently-formed carbonate is available for analysis in a water sample, the variation in concentration of carbonate is considered to be an approximate measure of the day to day photosynthetic activity. The amounts of bicarbonate alone would not gauge the daily photosynthetic activity since free carbon dioxide from the decomposition of the bottom soils is the first source utilized by the plants. The bicarbonates are, rather, a measure of the amount of carbon dioxide which is being "held in reserve" available for photosynthesis. While carbonates indicate to some extent the amount of daily photosynthetic activity, the bicarbonates are interpreted as indicative of the maximum photosynthetic activity possible. It will be recalled that at a few times during the year the reserve of bicarbonates is exhausted.

In Pymatuning Reservoir the greatest density of Cladocera is found in the Sanctuary lake; an intermediate density is found in the Middle lake; and the lowest, in the Lower lake. The amounts of particulate organic matter in the water and the amounts of organic matter in the bottom soils follow this same pattern. The highest concentration of bicarbonate is found in Sanctuary lake. This lake, moreover, receives the domestic sewage from the community of Linesville. In conjunction with this is the fact that Sanctuary is the shallowest of the three lakes so that nutrients from the bottom soils are being recirculated and made available for plant activity to an even greater degree than in the other two lakes.

Whether Cladocera utilize algae or detritus as food, if we view detritus as a decomposition product of algae, then photosynthetic activity can be considered as a measure of the amount of food available for Cladocera. Slobodkin (1954) found, in a laboratory-controlled experiment, a linear relationship between food supply and population size in *Daphnia obtusa*. On this basis, the greatest numbers of Cladocera should be found in the lake with the highest photosynthetic rate. A reduction of the three lakes to a common photosynthetic level (that is, to equal amounts of available food) should reduce their Cladocera populations to a common level. It is believed that this operation was performed statistically by accounting for that portion of the variation in densities associated with variations of pH and by regressing the Cladocera densities on concentrations of carbonates and bicarbonates—three chemical factors the concentrations of which are closely associated with photosynthetic activity. With the lakes thus reduced to a common level for amounts of available food the differences in densities of Cladocera between lakes did become non-significant. Therefore in a natural environment the primary factor which determines annual Cladocera densities and for which the Pymatuning lakes differ is food supply and the densities of Cladocera show a relationship to any chemical or physical factors which are, in turn, related to food supply.

SUMMARY AND CONCLUSIONS

1. Samples taken during the period June, 1952, to September, 1953, from the three lakes that constitute Pymatuning reservoir were analysed for numbers of Cladocera per liter, pH, and parts per million of dissolved oxygen, free carbon dioxide, bicarbonate and carbonate ion.

2. In numbers of Cladocera, particulate organic matter, and percentage of organic matter in the bottom soils, the three lakes—Sanctuary, Middle, and Lower—rate highest, intermediate, and lowest respectively.

3. Densities of Cladocera are correlated with the concentrations of oxygen, bicarbonate, and carbonate ions.

4. Analysis of variance revealed significant differences between lakes in densities of Cladocera, amounts of bicarbonate and carbonate ions.

5. Sums of squares and products associated with lakes for densities of Cladocera, carbonates, and bicarbonates, having been freed of the effects of variability between years and between levels of hydrogen ion concentration, were used in a multiple regression and covariance analysis.

6. As a result of this analysis the between-lakes errors of estimate were no longer significantly different from the errors of estimate for experimental error; the lakes were statistically reduced to a common level for concentrations of hydrogen ion, bicarbonate ion, and carbonate ion.

7. These three chemical factors are regarded as indexes of photosynthetic activity which is, in turn, considered to be a measure of the amount of food available for Cladocera.

8. The three lakes were, therefore, statistically reduced to a common level of photosynthetic activity or equal amounts of food; under these conditions the numbers of Cladocera did not differ significantly between lakes.

9. On the basis of these findings it was concluded that, in the environment provided by Pymatuning, densities of Cladocera are primarily determined by food supply and show a significant correlation with chemical and physical factors that are related to food supply.

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SURVIVAL AND TRANSMISSION OF A VIRUS CAUSING POLYHEDROSIS IN *MALACOSOMA FRAGILE*

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Introduction

A study of the occurrence and effects of an outbreak of the virus-caused polyhedrosis in a population of the Great Basin tent caterpillar *Malacosoma fragile* (Stretch) was reported earlier (Clark 1955). This study showed that the initial epizootic occurred late in larval development of the 1952 generation, and that the disease reappeared early in the larval development of the succeeding generation of 1953. *M. fragile* is a univoltine species, and since only the caterpillar stage is susceptible to infection, the virus obviously survived and was transmitted through a period of 9 to 10 months during which no susceptible stage of the insect was present. The means of survival and transmission of the virus between insect generations is of general interest in the study of the diseases of many hymenopterous and lepidopterous insects. Several investigators have studied this problem.

Most workers (Roegner-Aust 1949; Steinhaus 1949; Bergold 1953a; Bird 1955; Clark 1955) are agreed that the insect viruses are transmitted in some association with the egg. A second possible means of survival and transmission, as a contaminant on the host plant, seems to have been considered to a lesser extent. Balch and Bird (1944) considered the possibility that the virus of the European spruce sawfly, *Diprion hercyniae* (Htg.), overwinters on the host tree. Bird (1955), however, has concluded after several years study that transmission of the virus on the host tree does not occur to any significant degree. The writer (Clark 1955), on the other hand, found that the virus infecting *M. fragile* can survive the winter in the remnants of polyhedrosis-killed larvae on the host plant. He suggested that this overwintering virus may be a potential source of infection for the succeeding generation of insects.

The information reported in 1955, however, was limited to the demonstration of the viable and infectious virus on the host plant at the time of hatching of the larvae of the generation succeeding the outbreak of the disease. It was noted that this established the plant-contaminating virus only as a potential and not as an actual source of infection. The only food for developing larvae of *M. fragile* is the newly forming leaves of the host plant, and, since the host, *Ceanothus cordulatus* Kell., is deciduous, the virus could overwinter only on inedible portions of the plant. To infect the larvae, the virus must be moved onto new leaves and ingested.

The present paper reports observations and tests which indicate that the virus surviving as a contaminant on the host plant is an actual source of infection for hatching larvae.

Field Observations, 1953-1954

In April, 1953, a population of another tent caterpillar species, *Malacosoma californicum* (Pack.), infesting an abandoned orchard in Napa County, California, was used in producing large quantities of the virus for field tests of the application of the virus for control of the insect. The orchard used consists of two blocks, one of which contains about 50 trees arranged rectangularly, and lies about 100 yards from the second and smaller block of 19 trees arranged in two rows.

In producing the supply of virus in 1953, only the caterpillar colonies in the larger block of trees were used. Colonies throughout the larger block were collected and concentrated on about 20 trees. Not all the remaining trees were completely stripped of insects as some colonies were difficult to reach or were left for other reasons. No virus-killed larvae were found at this time. Following the concentration of colonies, the 20 trees were sprayed with a suspension of the polyhedral bodies in which the virus rods are occluded.[2] Eight days later, the infected insects were collected for the recovery of polyhedra. At the time of collection, scattered diseased larvae were left on the treated trees, as were the apparently disease-free larvae which remained on the untreated trees. The caterpillars infesting the 19 trees in the smaller block were not treated or disturbed.

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[2] The terms "polyhedral bodies" and "polyhedra" used in connection with the viruses that infect the nuclei of fat, blood, hypodermal, and trachal matrix cells of lepidopterous larva refer to the microscopic (0.5-15μ; Bergold 1953b) inclusion bodies characteristic of the disease. Working with *Porthetria dispar* (L.), *Porthetria monacha* (L.), and *Bombyx mori* L., G. H. Bergold in 1947 demonstrated that the polyhedra are not in themselves infectious, but occlude, as distinct components, the ultramicroscopic (20-70x200-400 mμ; Bergold 1953b) virus rods. Virtually all subsequent work on the nuclear polyhedroses of lepidoptera is ultimately based on Bergold's identification of infectivity with these rods. In studies of the application and the ecology of the polyhedroses the polyhedra, because of their microscopic visibility, are valuable tools in making diagnoses or gross approximations of concentration. The suspensions of polyhedra referred to in the present study are prepared by grinding polyhedrosis-infected larva in distilled water. Such suspensions are crudely purified by permitting the heavy polyhedra to settle on standing, and are then held under ordinary refrigeration until use.

The scattered treated and diseased larvae which were not collected died of polyhedrosis over a period of several days in April and May of 1953. *M. californicum* or *M. fragile* larvae dying of polyhedrosis ordinarily remain stuck to the host plant. Some of the larval remnants may adhere to the host plant by the prolegs and dry to a spongy or gummy substance with the integument intact. The integument of other larvae may break shortly after death and permit the liquified body contents, which carry the highly concentrated and infectious virus, to smear over leaves and twigs of the plant. In either case, these larval remnants and smears are the souce of the virus contaminating the plant.

In April, 1954, the orchard was re-visited with the intention of using it again to produce a supply of the virus. At this time, prior to any 1954 spraying of the virus, about 60 to 80 per cent of the insects were dead or dying of polyhedrosis. The caterpillar population was in the third and fourth instar. Larvae with symptoms of polyhedrosis were found over much of the larger block of trees, but colonies on many of these trees appeared to be virus-free. Inasmuch as the 20 trees which were sprayed in 1953 were not marked permanently, it could not be determined whether or not larvae killed by the virus occurred only on the treated trees. A diligent search of the 19 untreated trees, however, failed to reveal any larvae with virus symptoms.

Since the population of adult females depositing the eggs which hatched in 1954 was presumably the same for both blocks of trees, the occurrence of polyhedrosis only among the insects in the block of treated trees suggests that overwintering virus rather than virus transmitted with the egg was the source of infection in 1954.

Field Tests, 1954-1955

Neither the observations of the 1952-1953 natural epizootic or the fortuitous observations of the Napa orchard population of 1953-1954 were sufficiently controlled to permit definite assessment of the role of possible means of transmission other than host plant contamination. While both series of observations were suggestive, controlled tests were necessary. These tests involved the application of the virus in the fall to non-edible portions of the host plant followed by observations on the effect of the virus on the caterpillars of the generation of the following spring.

Site. The site selected for the test is in an area of *M. fragile* infestation on snowbrush, *Ceanothus cordulatus* Kell., near the Blue Canyon Airport, Placer County, California. This site is at an elevation of 5,280 feet along the western slope of the Sierra Nevada Mountains. The transition zone along the western slope is an important area of occurrence of *M. fragile* in California and *C. cordulatus* is the principal host of the insect in this zone (Clark 1956).

Methods. On November 18, 1954, the leaves were removed from the outer 25 inches on one twig of each of 10 snowbrush plants. After removal of the leaves, a suspension of the polyhedral bodies was throughly painted over the stripped twigs. Ten *M. fragile* egg masses were collected from plants in the immediate area, and one mass was tied just below the painted length of each treated twig. Since hatching larvae of *M. fragile* leave the egg mass and migrate fairly directly to the outermost tip of the twig, it was assumed that at the time of hatch, in June, 1955, the caterpillars would have to crawl long the length of the virus-treated stem to reach the forming leaves for feeding.

Weather. Among the weather factors which might be presumed to have an adverse effect on the virus contaminating the host plant through the winter are minimum temperatures, freeze-thaw cycles, and the washing effect of rain and snow. In view of the survival of the virus which is associated with the eggs, which is generally accepted, however, the washing would appear to be more important than the temperature because both the virus with the egg and that contaminating the plant are subjected to the same temperature fluctuations. The site of the test is in a natural area of occurrence of the insect in California and winter precipitation is fairly typical of that over much of the important range of the insect in the west-side Sierra region. In particular, the precipitation on the test side is ordinarily quite close to that on the area of the 1952-1953 epizootic. Pertinent weather data are given in Table I for comparison with other areas of tent caterpillar occurrence. Weather data are from the Blue Canyon Station, U. S. Weather Bureau, which lies within a quarter of a mile from the test site.

Controls. Observations on control insects were necessary to assess the influence of all sources of virus infections other than the virus smeared on the plant stems. The most obvious of such other sources is virus transmitted with the egg. Test

TABLE I. Temperature and precipitation data, Blue Canyon Station; U. S. Weather Bureau: Climatological Data, California, **58**: Nos. 11, 12; **59**: Nos. 1, 2, 3, 4, 5. U. S. Dept. Comm.

Month	TEMPERATURE °F				PRECIPITATION		
						Snowfall	
	Max.	Min.	No. days max. below 32	No. days min. below 32	Total	Total	Max. depth on ground
Nov........	69	20	0	4	6.7	1.1	T
Dec........	66	19	2	20	15.2	46.8	18
Jan........	61	19	10	23	7.9	67.3	19
Feb........	56	12	5	18	5.3	38.9	32
Mar........	60	19	0	20	4.0	10.7	30
April.......	60	17	4	20	9.4	81.2	29
May.......	77	28	0	7	1.9	4.8	21

and control eggs masses, therefore, were selected from the same field egg-mass population. The control egg masses were left undisturbed on the site of deposition. To control any possible effects of virus introduced from sources of which we might not be aware, the test was conducted within the immediate area of the control population. All test and control observations were made within a circle of 100 feet radius.

Results. To observe the results of the test, the area was visited five times between June 3, the date of the first hatching larva, and July 22, at which time the larvae on untreated plants had started to wander about prior to pupation. On each of these examinations, the approximate number of larvae in each test tent was recorded in relation to the number in the control tests. Each tent was examined for larvae or remnants of larvae showing indications of polyhedrosis and such larvae, when found, were returned to the laboratory for microscopic examination for confirmation of polyhedrosis. Similar examinations were made of control tents.

When the larvae of a colony of *M. fragile* die from polyhedrosis over a prolonged period of time so that few or none are dying at a given time, the dead larvae or larval remnants easily become lost in the tent debris or in the new webbing. This is particularly true when the deaths occur among the smaller larvae. The present tests and other field observations have shown that for this reason an examination of a number of tents for the presence of virus-killed larvae may give a rough approximation of current mortality rate; but the absence of any indications of polyhedrosis in a given tent at a given time is not evidence that the larvae in the tent are or have been virus-free. Thus virus-killed larvae may be present one week, absent the next, and present the third in a given tent. It is not possible to diagnose early infections of polyhedrosis in *M. fragile* with sufficient certainty to overcome this problem. The data presented, then, are reliable for a positive diagnosis of virus-present, but not necessarily for virus-absent in a particular tent at a given time. The degree to which virus infections occurred in the controls was ascertained by the repeated observations on many tents.

On the examination of June 3, only one larva had hatched. By June 14, the hatch appeared to be nearly complete and most of the broods had started to form tents. No evidence of polyhedrosis was found at this time.

When examined on July 6, a positive identification of polyhedra could be made from one or more larvae or larval remnants from 5 of 9 tents. The brood of the tenth egg mass had not formed a tent at the tip of the treated twig and was discarded from the test as not identifiable. Of the 9 test tents, one was rated as containing about the same number of larvae as in the control tents; the larvae of one had combined with the brood of a non-test tent on the same plant and could not be rated as to number present; and the remaining 7 were rated as containing few or very few larvae in comparison with the numbers in the control tents. A total of 32 control tents were examined on July 6 and no evidence of the virus was found.

The next examination was made on July 12. At this time, a positive identification could be made in 3 of the 9 tents. Of these 3, one established the virus in a tent which had not been positive on the preceding examination. The two examinations, then, showed the virus present in 6 of 9 or 66 per cent of the test tents. Recording the estimated number of larvae in 3 classes, 3 tents had no remaining living larvae, 3 had between 5 and 10 living larvae, and 2 had from 10 to 20 living larvae. As noted, the larvae of the ninth tent had combined with the brood of an untreated egg mass. This combined tent, one of the 6 with polyhedra present, contained between 30 and 40 living insects. Excluding the combined tent, the remaining 8 had a rough average of about 4 to 9 living larvae. Fifty control tents were examined for the presence of the virus. One or more larvae or larval remnants suspected of indicating polyhedrosis were found in 8 of the 50 tents. Of the 8 specimens, positive identification of polyhedra was possible in 4, or 8 per cent of the total examined. Ten of the control tents were removed for counts of the numbers of larvae. In comparison with the test tents, the numbers in the controls ranged from 11 to 92 with an average of 43 larvae per tent.

On the examination of July 22, there were no living larvae in any of the ten test tents. No new positive identifications of polyhedra could be made. In the controls, the maturing larvae had largely scattered and/or disappeared so that counts of larvae per tent were no longer practicable.

At this time the remaining test tents were cut and measured for length as a comparison of development with 21 randomly selected and measured control tents. Of the 10 test tents, 7 remained at this time. In addition to the 2 discarded for reasons noted previously, a third could not be measured because a compact tent had not been formed as a result of the brood having been destroyed early in development. The lengths of the 7 test tents ranged from 20 to 90 mm with an average of 52 mm. The lengths of the 21 control tents ranged from 55 to 140 mm with an average of 84 mm.

Discussion

The much higher rate of infection, the early reduction in numbers, and the retardation of tent development among test larvae as compared with the controls indicate that the virus smeared on the twigs in the fall survived the winter and was the source of infection for hatching larvae. The use of test egg masses taken from the same egg population as the controls and the maintenance of observations on the development of the control larvae in the immediate area of the tests provided a check on the influences of other possible sources of virus. Infection from such other sources as may have been available did not appear to be significant.

As reported earlier (Clark 1955), remnants of larvae of *M. fragile* killed by polyhedrosis adhere to the host plant through the winter and the virus within these remnants remains viable. That the virus within remnants and smears is an actual source of infection seems to be established in the qualitative sense by the present tests. As to what quantitative role this means of transmission may play—as contrasted to transmission of the virus in association with the egg, for example—is not known. No data on this question in the case of *M. fragile* and little or none on other species of insects susceptible to viruses appear to be available.

In view of the gregarious nature and restricted movements of young larvae of the Great Basin tent caterpillar, the quantity or volume and distribution of virus deposited by dying larvae would appear to be a dominant variable in the relative importance of transmission of the virus as a host plant contaminant. *M. fragile* larvae, in common with other members of the genus, are highly gregarious during the early and mid-stages of development. With light population densities, under which only a few plants of the stand are infested, there is little or no contact between larvae of different broods until the pre-pupation wandering of mature larvae. These mature larvae, however, are much more resistant to the disease than are the younger caterpillars. The virus surviving between generations on the host plant probably serves as a source of infection only for larvae developing from eggs deposited on the same plant. The probability of the larvae of an egg mass being infected by the virus contaminating the host plant would appear to be a function of the proportion of plants in the stand infested and contaminated by larvae of the diseased preceding generation and the proportion of the plants in the stand on which egg masses of the succeeding generation are deposited. Transmission of the virus as a host plant contaminant would appear to become increasingly important with increasing host population densities.

The amount of virus deposited is also important in that some loss undoubtedly occurs through winter weathering. Whether or not the amount of virus remaining in the spring is above the minimum needed to initiate infection would depend on the amount deposited the preceeding year.

Bird's (1955) negative results from his examination of the possible transmission by host plant contamination of the viruses infecting the sawflies *Neodiprion sertifer* (Geoff.) and *Diprion hercyniae* (Htg.), indicate that generalizations between insect species in this regard are not warranted. This is further substantiated by the writer's unpublished observations and data on the polyhedrosis of another lepidopterious species, the California oakworm *Phrygenidia californica* Pack. The occurrence of a polyhedrosis epizootic among a population of the oakworms in the San Francisco bay area prompted intensive examinations of the larvae of succeeding generations. No indications of generation-to-generation transmission of the virus were found. The distribution of the virus within the insect, the characteristics of the larvae dying of the disease, the characteristics of the host plant, and the weather all may be important in explaining the differences between different species of insects.

Summary

Previous work has shown that the virus causing polyhedrosis in the Great Basin tent caterpillar *Malacosoma fragile* (Stretch) can survive the winter on the host plant in the remnants of larvae dead of the disease. The present study is concerned with whether or not this virus is an actual

source of infection for the larvae of the succeeding generation.

Prior to field tests an observation that suggested that the virus wintering on the host plant can infect the larvae of the succeeding generation was made in Napa County, California. In 1953 several trees in an abandoned orchard were sprayed with the virus. Several diseased larvae of *Malacosoma californicum* (Pack.) died on the treated trees. A second block of trees in the orchard was left untreated. In the spring of 1954 about 60 to 80 per cent of the larval population in the treated block died of polyhedrosis. No evidence of virus was found in the untreated block.

Controlled tests were then conducted in a population of *M. fragile* infesting snowbrush, *Ceanothus cordulatus* Kell. in Placer County, California. These tests involved the application in the fall to inedible portions of the plant of a suspension of the polyhedral bodies in which the virus rods are occluded. This treatment was followed by observations on larvae that hatched the following spring from egg masses tied to the plant stem directly below the treated length.

In comparison with control insects the test larvae had a much higher rate of infection, were reduced in numbers and finally eliminated, and were retarded in the development of the tent. These results indicate that virus overwintering on the host plant is a source of infection for larvae of the next generation.

What quantitative role transmission of the virus as a host plant contaminant plays in relation to other means of transmission is not known. It seems reasonable to expect that this type of transmission becomes increasingly important with increasing population densities.

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BODY TEMPERATURES OF THREE SPECIES OF THAMNOPHIS

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The environmental temperature relationships of poikilothermic vertebrates are receiving more and and more attention as it is realized that they exhibit more control over their body temperature than was formerly thought. Recent evidence indicates that through behavioral thermoregulation, the body (or as usually registered, cloacal) temperature may be maintained above that of their immediate environment (or below) and there may be a characteristic cloacal temperature range for activity in different forms.

Throughout 1950, cloacal temperatures were recorded for all captures from a large population of three species of garter snakes, the common garter snake, *Thamnophis s. sirtalis,* the ribbon snake, *Thamnophis s. sauritus,* and Butler's garter snake, *Thamnophis butleri,* near Dixboro, Washenaw County, Michigan (for a description of the area, see Carpenter, 1952). Temperatures were also taken simultaneously for air, ground surface, soil, and other places depending upon the particular situation.

The following procedure was used in recording the cloacal temperature of the garter snakes. A quick-reading Schultheis thermometer (Bogert 1949) was used for all readings. The bulb on this instrument is small enough to enter the cloaca of the smallest garter snake. On sighting a snake at a distance in the field, the thermometer was made ready for immediate use and the cloacal temperature was taken immediately after capture by thrusting the bulb out of sight into the cloaca. Cloacal temperatures were always taken within 10 seconds after capture.

The air temperature was recorded approximately 3 feet above the ground. In taking the ground surface temperature, the thermometer was laid on the ground simulating the position of the snake. The thermometer was thrust into the ground about one inch for obtaining soil temperatures.

When the cloacal temperatures of the three snakes for all seasons are plotted against ground surface temperatures, air temperatures or soil temperatures, one pattern is generally apparent, that is, more than 70 per cent of the cloacal temperatures fall between 20°C and 30°C. At the lower environmental temperatures, the cloacal temperatures are usually higher than, and at the higher environmental temperatures the cloacal temperatures are usually lower than those of the environment (Figs. 1, 2, 3). The mean cloacal temperatures for the three species are close, being 25.6°C for *T. s. sirtalis,* 26°C for *T. s. sauritus* and 26.1C° for *T. butleri* (Table I).

The greatest similarity between cloacal and environmental temperatures exists between the former and the ground surface temperatures (Table I). This is understandable, in that the snake is most closely associated with this region of the habitat.

Sex and size differences are only slight and are not consistent for the three species (Table I). Though these differences might prove to be significant, further study will be necessary.

The warmer summer temperatures in Michigan generally occur in July and August and this is reflected in a higher mean cloacal temperature for all three species during this period as compared to early summer (Table I).

The above data suggest that these snakes, though greatly influenced by environmental temperatures, are able to regulate their body temperature. This type of control has been called behavioral thermoregulation. Evidence for this type of behavior has been frequently observed in *Thamophis* and other reptiles as well.

The garter snakes are known to come out of hibernation for short periods during mild spells in winter and early spring and sun themselves. This behavior is frequently observed in the early morning on cooler days during the summer. This sunning is associated with the raising of the body temperature to the activity level. An excellent example of this type of behavior has been described by Pearson (1954) for a lizard living at high altitudes in Peru. Garter snakes captured with cloacal temperatures below 20°C are usually

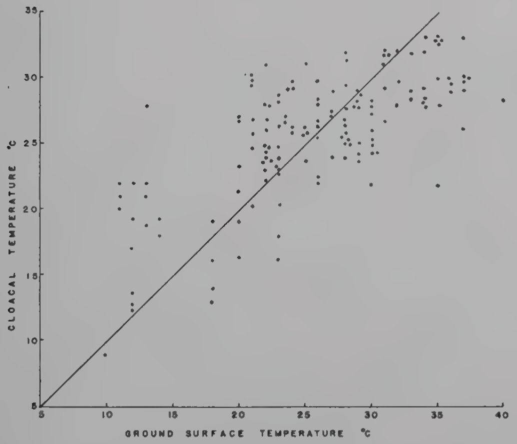

FIG. 1. Scatter diagram showing relationship between ground surface temperatures and the cloacal temperatures of *Thamnophis s. sirtalis* near Ann Arbor, Washtenaw County, Michigan, 1950.

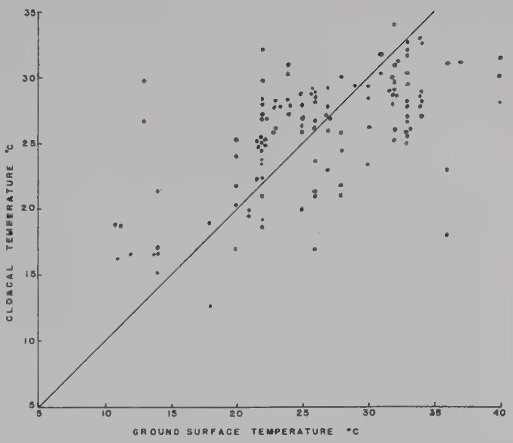

FIG. 2. Scatter diagram showing relationship between ground surface temperatures and the cloacal temperatures of *Thamnophis s. sauritus* near Ann Arbor, Washtenaw County, Michigan, 1950.

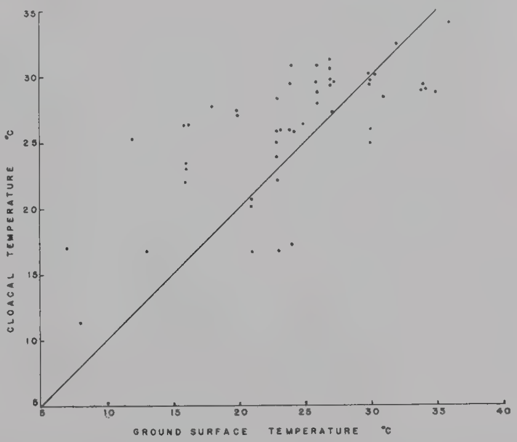

FIG. 3. Scatter diagram showing relationship between ground surface temperatures and the cloacal temperatures of *Thamnophis butleri* near Ann Arbor, Washtenaw County, Michigan, 1950.

TABLE I. Summary of data for cloacal temperatures of garter snakes, and for air temperatures, soil temperatures and ground surface temperatures near Ann Arbor, Washtenaw County, Michigan, 1950. (Mean, standard error of the mean, and range)

	Thamnophis		
	sirtalis	*sauritus*	*butleri*
Number	144 (76 M, 68 F)	123 (50 M, 73 F)	54 (32 M, 22 F)
Cloacal temperatures, °C			
Mean	25.60 ± .40 (9.0-35.0)	26.0 ± .41 (12.6-34.0)	26.1 ± .63 (12.4-34.0)
Mean, males only	24.07 ± .61 (9.0-33.0)	25.05 ± .64 (12.6-33.0)	26.30 ± .79 (12.4-34.0)
Mean, females only	27.32 ± .49 (12.4-35.0)	26.72 ± .42 (15.2-34.0)	25.94 ± 1.02 (16.6-32.0)
Mean, body length ≤ 30 cm	26.20 ± .78 (18.0-33.0)	24.30 ± 1.03 (16.6-33.0)	25.28 ± 1.29 (16.6-32.3)
Mean, body length ≥ 30 cm	25.58 ± .45 (9.0-35.0)	26.29 ± .45 (12.6-34.0)	26.46 ± .70 (12.4-34.0)
Mean, April-June	25.47 ± .58 (9.0-33.0)	26.03 ± .47 (16.2-34.0)	25.65 ± .83 (12.4-34.0)
Mean, July-September	28.42 ± .44 (22.2-35.0)	26.83 ± .65 (15.2-33.0)	29.51 ± .45 (27.0-32.3)
Environmental temperatures, °C			
Mean, air	21.64 ± .61 (7.0-32.0)	22.28 ± .55 (7.0-32.0)	20.94 ± .80 (7.0-29.0)
Mean, ground surface	25.64 ± .56 (10.0-40.0)	26.23 ± .18 (11.0-40.0)	24.21 ± .91 (7.0-36.0)
Mean, soil	20.67 ± .23 (5.0-36.0)	22.38 ± 1.04 (6.0-36.0)	19.26 ± .83 (7.0-32.0)

sluggish in comparison to those with temperatures above this point. Body temperatures of snakes in hibernation are also above those of the immediate environment (Carpenter 1953).

Regulation at high environmental temperatures in *Thamophis* was observed to involve retreat to shade (they were much less active in the open on hot days) and also climbing into bushes. All three species were observed up in bushes (as high as 6 feet for *T. s. sauritus*) during the hottest days (Carpenter 1952).

The lethal temperature for *Thamnophis sirtalis* and *Thamnophis radix* was given as approximately 41°C by Lueth 1941; his snakes died in 48 hours in constant temperature chambers. This is probably about the same for all three *Thamnophis* in this study. Though lethal temperatures were nearly reached (40°C) on the ground surface, the highest cloacal temperature recorded (35°C) was well below this. Many active lizards have been recorded with body temperatures as high as 43°C (Bogert 1949, and personal observations), a temperature which would be likely to kill many snakes.

The term used by Bogert (1949) for the mean body temperature is the *preferred body temperature* (PBT) and can be applied to the mean body temperatures for the three *Thamophis.* Since the majority of body temperatures fall between 20°C and 30°C, this range could be called the *thermoactivity range* (TAR) for these snakes. When the data for the *Thamnophis* are plotted as a histogram (Fig. 4) this range is evident. Individuals above and below this range are generally much less active. Extended field observations throughout the three years' period of study (1948-50) indicated that few snakes are active below 20°C and above 30°C. Above 30°C their position generally indicates behavior to avoid heat. At temperatures decreasing below 20°C they become increasingly sluggish.

The slight differences in PBT between the three species of *Thamnophis* studied here can be correlated to seasonal activity and temperature tolerance. *T. s. sirtalis,* having the lowest PBT, is active earlier and later in the season than the other two forms and has a much greater geographical range to the north, which would indicate a greater tolerance to low temperature.

SUMMARY

Cloacal temperatures recorded for a large population of three species of garter snakes (*Thamnophis s. sirtalis, Thamnophis s. sauritus,* and *Thamnophis butleri*) in Michigan indicate that some thermoregulation is present in these forms. During cold and hot weather respectively cloacal temperatures are above and below the immediate environmental temperatures. More than 70 per cent of all records for each species had cloacal temperatures between 20°C and 30°C. The mean cloacal temperature for all *T. s. sirtalis* was 25.6°C, for all *T. s. sauritus* 26°C, and for all *T. butleri* 26.1°C, indicating no significant species differences. These cloacal temperature are more closely correlated with the temperature at the ground surface than with air temperature above or soil temperature below. These snakes exhibit temperature control through behavioral thermoregulation; sunning in cool weather and seeking cooler areas in hot weather.

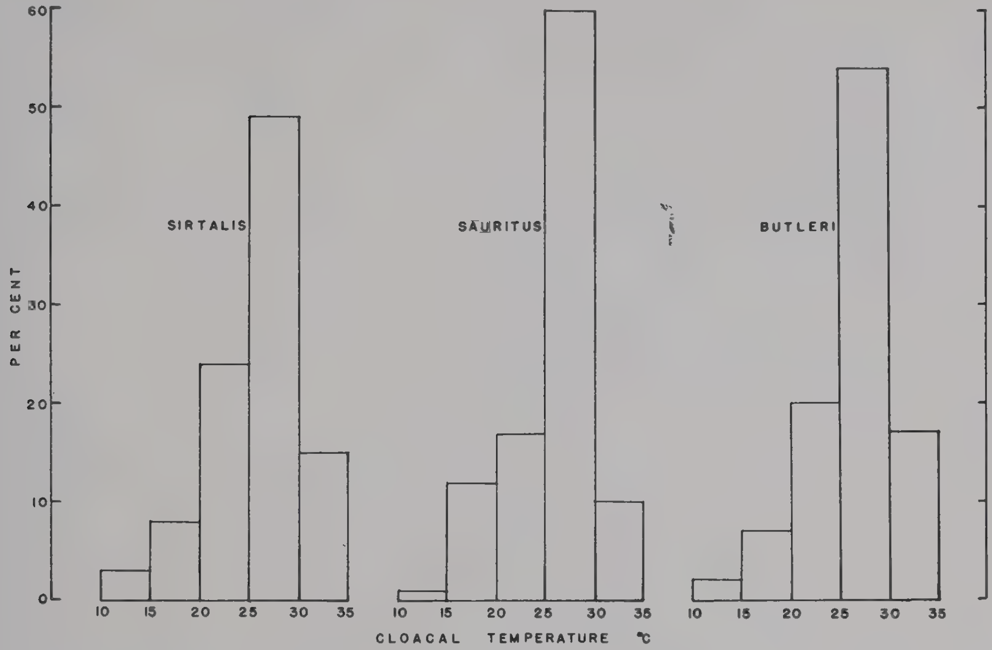

Fig. 4. Distribution (as per cent of total) of cloacal temperature readings for three species of *Thamnophis* near Ann Arbor, Washtenaw County, Michigan, 1950.

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GROWTH OF HARDWOODS AFTER CLEAR-CUTTING LOBLOLLY PINE

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Because of the direction of plant succession, a hardwood understory is characteristic of mature loblolly pine stands (Oosting 1942, Wells 1928). Modern logging destroys much of the aerial portions of that understory, but the roots nearly always remain. The vigorous hardwood sprout growth that arises in clear-cut areas competes directly with whatever pine seedlings become established and is a serious obstacle to successful even-aged management of loblolly pine. This sprout stand merits careful study so that its influence on pine reproduction can be evaluated accurately and effective methods can be devised for its control.

In some parts of clear-cut areas, the hardwoods have been severely damaged and the litter is well-disturbed, providing a favorable seedbed for pine germination (Pomeroy 1949, Trousdell 1950). By contrast, in thickets of small hardwoods that are not disturbed by logging, the litter is also undisturbed and few pine seedlings become established. Under large hardwoods, seedbed conditions may be more favorable, but the seedlings that do become established have very little chance of penetrating the overtopping canopy. Chapman (1945) shows that the presence of undisturbed hardwoods can preclude the development of a dominant pine stand.

The composition of the stand that develops after logging depends on the comparative densities and growth rates of pine seedlings and hardwood sprouts. Some of the required information for predicting stand composition and short-term succession has been obtained from a study of the growth rates of hardwood sprout clumps and the increase in area covered by hardwoods in clear-cut areas in the Bigwoods Experimental Forest.[1] Clear-cuttings of pure, mature loblolly pine stands in 35-acre tracts, leaving scattered seed trees or uncut strips, were made in the experimental forest every year from 1946 to 1952. Thus, ideal conditions existed on this area for studying the development of hardwoods on upland sites after clear-cutting. Collection of the required data began in 1951.

The new hardwood growth is composed not only of sprouts from the trees and shrubs destroyed in logging but also of seedlings of trees, shrubs, and vines that are adapted to the open condition. It was impractical, and thought unnecessary, to study each one of this large number of species. Instead, two complementary methods of study were adopted. The first dealt with the area occupied by the new hardwood growth in relation to time since cutting, soil characteristics, and seedbed preparation. The second dealt with the height growth and lateral expansion, in relation to the same factors of age, soils, and seedbed, of five species of hardwoods sprouts deemed the most serious competitors of pine seedlings.

AREA OCCUPIED BY NEW HARDWOOD GROWTH

The area occupied by the crowns of the new hardwood growth was measured on square, 1/10-acre plots by the line-intercept method. Three soil groups, two soil surface conditions, and several ages of hardwood sprout growth (based on time since clear cutting of the pine stand) were sampled by 67 plots, distributed as shown in Table I. The plots were located in areas of uniform surface drainage and subsoil consistency by means of a soils map[2] of the experimental forest. The soil classification was checked on each plot. Soil surface conditions were burned and unburned. All burning was done in late summer, within 1 year after logging.

TABLE I. Distribution of plots in relation to surface drainage, subsoil consistency, soil surface condition, and years since harvest cutting

Years since harvest cutting	WELL-DRAINED FRIABLE SOILS		WELL-DRAINED PLASTIC SOILS		POORLY-DRAINED PLASTIC SOILS	
	Burned	Not burned	Burned	Not burned	Burned	Not burned
	No. plots	*No. plots*	*No. plots*	*No. plots*	*No. plots*	*No. plots*
0............	3	2	..	..	..	..
1............	2	5	7	6	4	5
2............	4	..	..	..	..	..
3............	3	5	3	..	7	..
4............	..	..	..	2	..	2
5............	..	..	2	4	..	1
Total plots..	12	12	12	12	11	8

Plots were established and initial measurements were made in late summer, after stem elongation was complete or nearly so. Ten line-transects were run across each plot. Both ends of each transect were permanently marked to permit remeasurement. For each transect measurement, a 1-chain tape was stretched across the plot and the distances intercepted by all hardwood crowns were recorded. All plots were remeasured at the same time in the next year.

Generalized curves of increase in hardwood area over years since harvest were derived from the data by the method of least squares, and the significance of differences was determined by appropriate statistical tests. Figure 1 shows the trends of increase in hardwood area on each soil group-surface condition combination, beginning with an initial coverage of 10 per cent, which was typical of fresh clear-cuttings in the experimental forest.

In the absence of burning, hardwood cover increased fastest on the poorly-drained soils, probably because moisture is plentiful on these soils during most of the year. The slowest increase occurred on the well-drained plastic soils. With less moisture available, the poor physical characteristics of these soils probably are the principal controlling factor in the growth of the hardwoods. The rate of increase was intermediate on the well-drained friable soils, which were fine sandy loams, with some loamy fine sand, 12 to 24 inches deep underlain by sandy clay. These excellent physical characteristics may have been partly offset by the free internal drainage.

After burning, hardwood area increased fastest on the well-drained friable soil, slowest on the poorly-drained plastic soil, and at an intermediate rate on the well-drained plastic soil. Burning increased the rate of hardwood development on the two well-drained soils by about equal amounts, and decreased it on the poorly-drained soil by about twice as much. The increased growth following burning on the well-drained soils was probably caused by the improved fertility following release of mineral nutrients and nitrogen from the

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[1] Maintained in Hertford County, N. C., by the U. S. Forest Service in cooperation with the Camp Manufacturing Company, Inc., Franklin, Virginia.

[2] Prepared by W. D. Lee, Soil Specialist, N. C. Agricultural Experiment Station, N. C. State College, Raleigh, N. C.

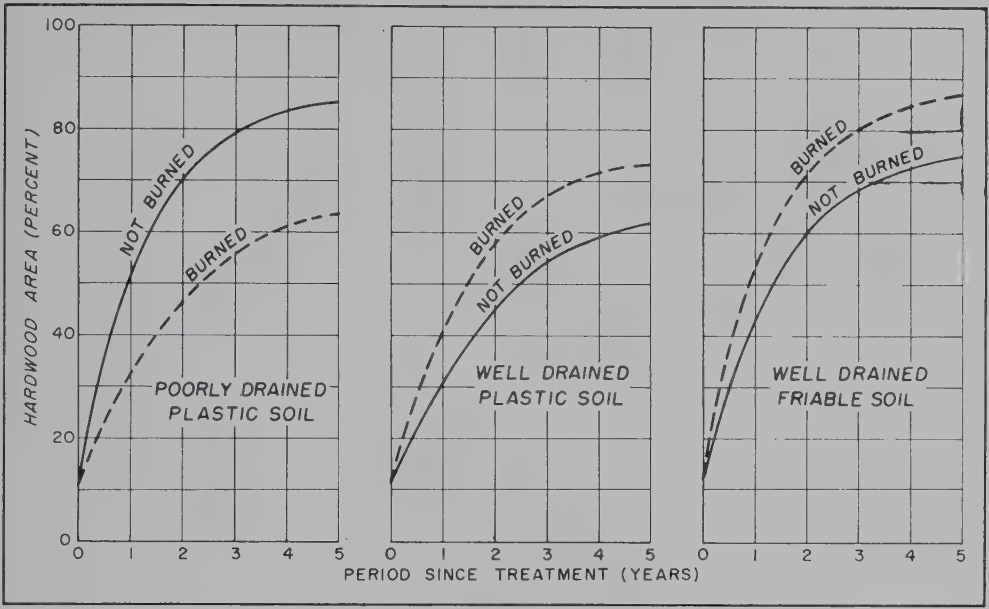

FIG. 1. Development of hardwood cover by soil group and surface treatment.

litter. The decreased growth on poorly-drained soils is less readily explained. Possibly aeration was poorer after burning because these soils are more likely to puddle and pack under exposure.

GROWTH OF INDIVIDUAL SPROUT CLUMPS

Sweetgum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), the red oak group (*Quercus* spp.), dogwood (*Cornus florida* L.), and waxmyrtle (*Myrica cerifera* L.) were chosen for the study of individual sprout clumps. The red oak group was composed mainly of southern red oak (*Quercus falcata* Michx.), but also included black (*Quercus velutina* Lam.), scarlet (*Quercus coccinea* Muenchh.), and water oak (*Quercus nigra* L.). Eight hundred and forty-nine sprout clumps of these species were distributed, although not equally, among the three soils groups, the two surface conditions, winter and summer cutting, and were up to 4 years of age. Measurements made on each clump were:

1. Height of the dominant sprout at each age up to the present;
2. Width of the clump at its widest point in the vertical plane;
3. Height to the point of crown width measurement;
4. Diameter of the parent stump.

Sprout clumps of the selected species were measured as encountered in strips 40 links wide until 30-40 clumps of the most numerous species had been recorded for each combination of soil and treatment. Thus, the total length of strip ranged from 2 to 9 chains among the different conditions sampled. Within each set of conditions, however, each species was measured over the entire strip length. The initial measurements were made in late summer. They were repeated 1 year later so that a better range of crown width and crown height would be obtained.

All combinations of environmental conditions and treatment could not be compared because they do not exist in the experimental forest. For example, since all burning was done in the late summer, only the effect of late summer burning could be determined. Sufficient sprout clumps of some species were not found within some areas examined, which rules out other comparisons. That was particularly true with waxmyrtle and dogwood on the poorly-drained plastic soil.

The data were analyzed by the method of covariance. For each species, a relation of height of sprout clumps to age and stump diameter was obtained that was independent of environmental influences. The relation was used to adjust the mean heights under the several sets of environmental conditions to the general means of age and stump diameter, so that all comparisons were, in effect, between sprout clumps of the same age and stump diameter. The adjusted mean heights and a summary of significant comparisons are shown in Table II.

TABLE II. Adjusted mean heights of sprout clumps of five species and summary of significant differences

FACTORS AFFECTING SPROUT GROWTH				ADJUSTED MEAN HEIGHT OF SPROUTS					35-acre tracts sampled
Season of		Surface after treatment	Soil group						
Clear cutting	Burning after clear cutting			Sweet-gum	Red maple	Red oak	Dog-wood	Wax-myrtle	
				Feet	*Feet*	*Feet*	*Feet*	*Feet*	*Number*
Summer	Summer	Burned	WP	3.86	4.28	3.01	....	2.71	2
Winter & Summer†	Summer	Burned	WF	5.30	4.92	4.39	3.71	2.67	2
Summer	Summer	Burned	PP	3.33	3.57	1.99	....	....	1
Summer	None	Not burned	WP	4.74	3.97	2.90	3.94	....	1
Summer	None	Not burned	WF	4.49	4.18	3.17	3.89	3.17	3
Summer	None	Not burned	PP	4.00	3.58	3.21	....	....	1
Winter	None	Not burned	WP	4.77	4.90	3.61	4.52	....	1
Winter	None	Not burned	WF	....	....	6.20	3.84	3.02	1
Winter	None	Not burned	PP	4.71	5.16	3.30	....	....	1
SIGNIFICANCE OF DIFFERENCES AMONG ADJUSTED MEAN HEIGHTS									
Any season	Summer	Burned	WP vs WF	**	**	**		—	
Any season	Summer	Burned	WP vs PP	—	**	*			
Any season	Summer	Burned	WF vs PP	**	**	**			
Summer	None	Not burned	WP vs WF	—	—	—	—		
Summer	None	Not burned	WP vs PP	—	—	—			
Summer	None	Not burned	WF vs PP	—	*	—			
Winter	None	Not burned	WP vs WF			**	—		
Winter	None	Not burned	WP vs PP	—	—	—			
Winter	None	Not burned	WF vs PP			**			
Summer	Summer	B vs NB	WP	—	—	—			
Summer	Summer	B vs NB	WF	**	**	**	—	*	
Summer	Summer	B vs NB	PP	—	—	*			
Summer vs Winter	None	Not burned	WP	—	**	—	—		
Summer vs Winter	None	Not burned	WF			**	—	—	
Summer vs Winter	None	Not burned	PP	*	**	—			

†Two 35-acre tracts clear cut in different seasons.
WP, well-drained plastic soils
WF, well-drained friable soils
PP, poorly-drained plastic soils

B, burned
NB, not burned
S, summer cut
W, winter cut

**, significant at 1% level
*, significant at 5% level
—, not significant
Blank, no comparison available

Only a limited number of comparisons could be made with waxmyrtle and dogwood because of their erratic occurrence. Of the available comparisons, only one was significant—waxmyrtle sprouts on the well-drained friable soils grew more slowly with burning than without burning.

Among the three more important species, the outstanding result was that burning significantly increased their height growth on the well-drained friable soils. Burning did not affect their height growth on the well-drained plastic soils, and significantly reduced height growth only of red oak on the poorly-drained plastic soils. Thus, these three species responded to soils in different ways without burning; but after burning they all grew fastest on the well-drained friable soils, slower on the well-drained plastic soils, and slowest on the poorly-drained plastic soils.

Wherever a comparison could be made, sprouts following winter harvest were found to grow as fast or faster than sprouts following summer harvest. Because burning was done only in late summer, comparisons of sprout growth following winter and summer harvest are available only for unburned seedbed conditions.

Figure 2 shows the trends of height growth for sprouts arising after winter cutting, without fire, from 1-inch stumps on the well-drained plastic soil group. Similar sets of curves can be drawn for each stump diameter on each of the sampled combinations of conditions. The combination used for Figure 2 is probably the most frequently encountered in the coastal plain of Virginia and North Carolina.

The parent-stump diameter significantly affected the growth of sprouts in all species. The majority of stumps studied were less than 4 inches in diameter. Up to 5 years of age, sprouts from larger stumps grew faster in height. A 1-inch difference in stump diameter was associated with a 0.5-foot difference in the height of sweetgum, red maple, and red oak sprouts, a 0.3-foot difference in the height of dogwood sprouts, and an 0.8-foot difference in the height of waxmyrtle sprouts.

The relations of crown width and crown height to total height of the sprout clump were positive

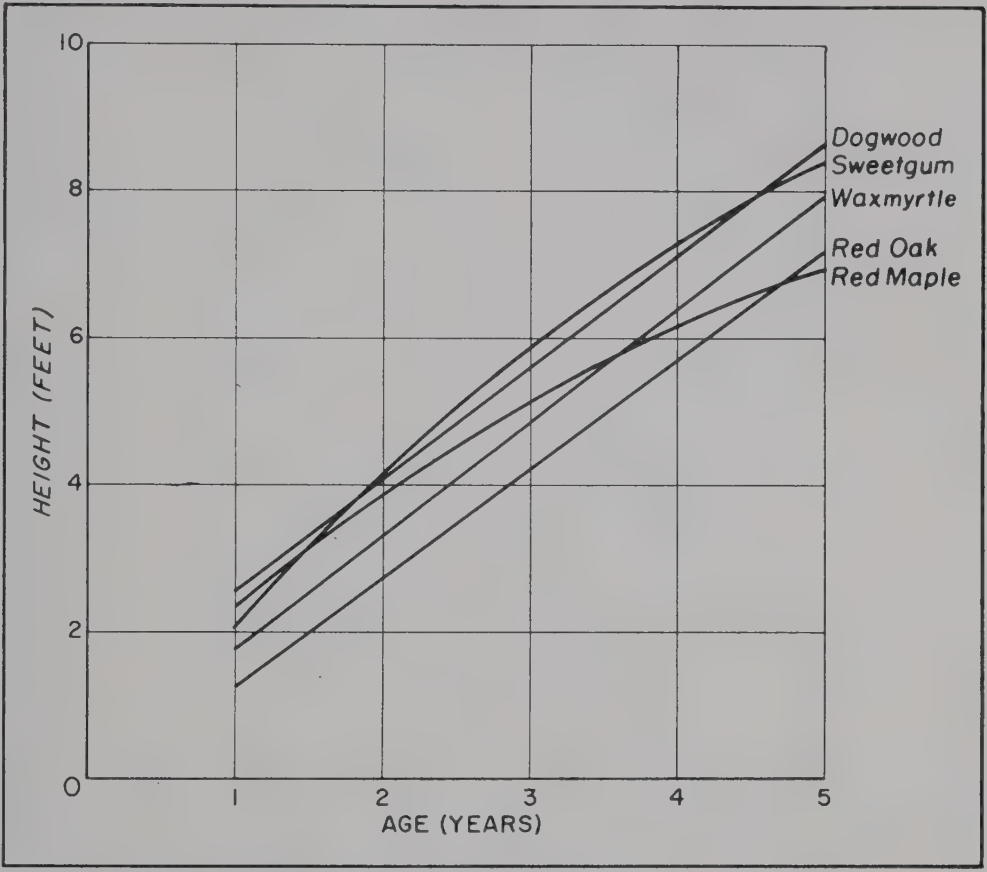

FIG. 2. Relation of height to age of hardwood sprout clumps of five species.

and linear for all species except sweetgum. Apparently one sprout quickly assumed dominance in that species at the expense of others in the clump, so that lateral expansion remains practically at a standstill after an initial spurt of growth until a tree-like crown develops on the dominant sprout. Sprouts of the other four species expand laterally in proportion to their height and thus retain the sprout clump form throughout at least the first 5 years. Differences in environmental conditions and treatment had no effect on these relations. There is no reason to suppose that sprout clumps of a given species have a different form under one set of conditions than under another, providing the amount of light is not greatly different.

Of particular interest are the frequencies[3] of occurrence of the species with respect to soil groups. These are presented in Table III. Because the length of strip was the same for each species, the frequency of occurrence of the species in the strips is an estimate of that in the area as a whole. With improved drainage and lighter texture, sweetgum and red maple became relatively less numerous, whereas red oaks, dogwood, and waxmyrtle became more so. Particularly notable is the virtual absence of dogwood and the scarcity of waxmyrtle on the poorly-drained heavy soils.

These findings agree in a general way with those of other studies. Ferrell (1953) found that sweetgum seedlings grew faster on lighter soil but survived better on heavier soil. Coile (1950) found that understory sweetgum occupied more area on coarse-textured soils of good site quality, which could result from either growth or frequency of occurrence. Bormann (1953) and Wenger (1952) found better survival of sweetgum seedlings on heavier soils.

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[3] "Frequency" is used here in the statistical sense: the ratio of the number of individuals falling within a single class to the total number classified.

TABLE III. Frequencies of occurrence of sprout clumps of five hardwoods species according to major soil differences

Species	Poorly-drained plastic soil	Well-drained plastic soil	Well-drained friable soil
	Per cent	*Per cent*	*Per cent*
Sweetgum......	41.5	39.0	26.0
Red maple.....	43.0	39.0	26.0
Red oaks......	12.0	10.0	21.0
Dogwood......	0.5	5.0	15.0
Waxmyrtle.....	3.0	7.0	12.0
Total.......	100.0	100.0	100.0

In the present study, sweetgum occurred with greater frequency on the heavier soils but grew as fast or faster on the lighter soils. Red maple also grew better on the lighter soil but was more numerous on the heavy soil. The red oaks also grew best on the well-drained friable soil, but in contrast to sweetgum and red maple they were also somewhat more numerous there. Ferrell (1953) found that red oak grew faster on lighter than on heavier soils and that survival increased slightly with an increase of available soil moisture of from 4 to 20 per cent. Available soil moisture is difficult to relate to soil texture, but with respect to growth, the findings of both studies are similar.

The much greater frequency of occurrence of dogwood on the light soil compares well with Ferrell's (1953) finding that the survival of dogwood was much lower on heavy than on light soils. Waxmyrtle also was more numerous on the light soil, but the data are too meager to furnish any information about its growth in relation to soils.

The work of Bormann (1953), Ferrell (1953), and Wenger (1952) was done with 1- and 2-year-old seedlings rather than with sprouts from older trees, and Coile (1950) dealt with the general run of understory sizes and growth forms. Since the several findings corroborate each other so well in spite of the difference in research methods and materials, the observed responses to soil factors may be considered as characteristic of the species.

INTEGRATION OF FINDINGS

Although sweetgum, red maple, and red oak are the most numerous competitors of pine seedlings, many other species of hardwood trees, shrubs, and vines become established after harvest clear-cutting. Because these species undoubtedly vary greatly in their responses to environmental conditions, their aggregate response, expressed by total hardwood area, is not likely to agree with the response of any one species. Thus, the effects of soils on the height growth of sprout clumps do not agree in any respect with the effects of soils on the rate of hardwood area growth, in the absence of burning.

After burning, both hardwood area and sprouts of sweetgum, red maple, and red oak responded to soil differences in the same way, growing faster on the well-drained friable soil, more slowly on the well-drained plastic soil, and slowest on the poorly-drained plastic soil. The lack of agreement without burning and the close agreement after burning suggest that the interaction of burning with soils influences the growth of all species so strongly that species differences are largely obscured. All burning in the experimental forest was done from late August till early October. Consequently, although it is called "summer" burning, the rate of growth is probably more typical of sprouts from dormant season fires than from fires earlier in the growing season (Wenger 1953). Chapman (1952) recommended that kind of fire for seedbed preparation in loblolly pine mangement. Very little if any sprouting occurs after the fire, so that seedlings start even with the sprouts in the next spring. However, in considering use of the treatment, its effect on well-drained soils should be taken into account. If a poor pine seed crop is in prospect, or if the area already bears a heavy stand of small hardwoods that would be multiplied by sprouting after the fire, the hardwood problem might be seriously aggravated. Some other method of seedbed preparation should be considered for these cases, because any positive remedy for the failure of reproduction after clear-cutting is difficult and expensive.

The comparison between hardwood area growth and sprout height growth is also worth while. Since the area occupied by a sprout clump is a function of crown width, and crown width is closely related to total height, it might be expected that hardwood area growth would follow about the same trend as sprout height growth. However, hardwood area increased rapidly in the early years and slowed down abruptly after the third year (Figure 1), while individual sprout clumps grew in height at the same rate or slowed down only slightly during the first 5 years (Figure 2). The divergence does not seem so contradictory, however, when the growth of sprout clumps in the aggregate is considered. A certain potential hardwood area exists in a newly clear-cut tract, more or less depending on the extent to which the hardwood roots were destroyed by logging or other treatments. During the first year, the majority of sprout clumps are fairly well isolated and virtually all growth is reflected in an increase in area occupied. As the sprout clumps expand, at a constant rate, more and more crown closure occurs, and area growth must drop as complete crown closure is approached. That condition apparently is reached in about the third year. Height growth, however, apparently is not seriously retarded by crown closure and continues at nearly the same rate.

The course of development of the hardwoods also suggests what effect they may have on pine seedlings. The three conditions of hardwood vegetation in clear-cut areas occur in parcels of all different sizes from a few square feet up to substantial proportions of an acre, completely intermingled over the clear-cut tract. Since that pattern is a result of logging and sometimes other treatments, and since the bulk of the pine is established in the first year after clear cutting (Trousdell 1954), the composition of the future stand is fixed as early as one growing season after clear-cutting or final treatment. However, it cannot be clearly seen until the initial surge of sprout growth is past. According to the trend of hardwood area increase found in this study, vegetational conditions are fairly stable by the end of the third growing season. A reliable estimate can then be made of the stocking of free-growing, potentially dominant pine seedlings. Generally, seedlings that are not overtopped by that time have a good chance of staying ahead of the hardwoods. A comparison of relative positions and growth rates of the pine seedling and its immediate hardwood competitor will help in judging the doubtful cases. If poor-prospect seedlings and the kind of hardwood competition (sprout clumps or larger trees) are also recorded, the stocking survey will also show what cultural treatments are needed to bring the stocking up to some prescribed standard.

Summary

The hardwood sprout growth that arises after clear-cutting loblolly pine stands was studied in two ways: (1) in the aggregate by determining the rate of increase in area occupied by hardwood sprouts in relation to gross soil differences and burning after logging; and (2) individually by determining the rate of height growth in relation to gross soil differences, burning after logging, season of logging, and parent-stump diameter of sweetgum, red maple, the red oak group, dogwood, and waxmyrtle.

The area covered by hardwoods increased sharply in the first and second years following clear-cutting and slowed down rather abruptly in following years. Without burning, growth was fastest on poorly-drained plastic soil, slower on well-drained friable soil, and slowest on well-drained plastic soil. Burning increased the rate of area growth on the well-drained soils and decreased it about twice as much on the poorly-drained soils so that after burning growth was fastest on the well-drained friable soil, slower on the well-drained plastic soil, and slowest on the poorly-drained plastic soil.

Individual sprout clumps of the species mentioned varied in their responses to soils without burning and to season of cutting. After burning, sweetgum, red maple, and the red oaks responded to soil differences in the same way as the area covered by hardwoods, growing fastest on the well-drained friable soils, slower on the well-drained plastic soils, and slowest on the poorly-drained plastic soils.

Height growth of red oak, dogwood, and waxmyrtle sprouts continued at a constant rate during the initial 5-year period; that of sweetgum declined slightly with each succeeding year, and that of red maple declined a greater amount in each succeeding year throughout the period. Crown width and crown height were directly related to total height in all species except sweetgum. Height growth was significantly related to diameter of parent stump in all species.

Sweetgum and red maple were more numerous in relation to the other species on the heavier soils, and red oak, dogwood, and waxmyrtle were more numerous on the light soils. Dogwood and waxmyrtle were very scarce on the heaviest poorly-drained soil.

These findings were compared with the growth responses and survival of the same species reported by other workers and agreed with them quite closely.

The probable effects of the hardwoods on pine seedlings were pointed out.

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A STUDY OF SOME FEATURES OF GROWTH AND REPRODUCTION OF *PINUS PONDEROSA* IN NORTHERN IDAHO[1]

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Introduction

This study was designed to compare some growth and reproductive features in individuals of *Pinus ponderosa* Laws. growing on different habitat types and to compare the growth of different age-classes of this species. Measurements were made of the growth of needles, stem apices, stem radii, and staminate cones, and records made of season of needle fall and pollen shedding. Owing to microclimatic compensation, the usual elevation sequence of the two plant communities in which the trees were found was reversed; the community usually found at the higher elevation along a mountain slope occurred almost 700 m lower than the community normally confined to the lower range in elevation; thus, the study affords a comparison of the phytosociologic relations versus altitude as these affect phenology.

Several quantitative studies have been made of growth in this tree but none has related growth to specific plant associations. MacDougal (1924) working in northern Arizona compared radial growth of young and old trees of *P. ponderosa.* Fowells (1941) conducted a study in which height growth, radial growth, and needle growth of this tree were compared at different elevations in the Sierra Nevada. Daubenmire and Deters (1947) have studied radial growth and needle elongation in this species in an arboretum. Daubenmire (1946) included *P. ponderosa* in a study of radial growth of conifers at different altitudes on Thatuna Ridge, which is in the same general area as that in which the present study was conducted. Two other papers by Daubenmire (1949, 1950) present evidence concerning the initiation of cambial activity in this species. Jackson (1952) records the results of a radial growth study of planted *P. ponderosa* in the Georgia piedmont. A noteworthy contribution to studies of this tree has been made by Roe and Boe (1950) who have compiled a bibliography including other plenologic studies of the species.

Methods

Description of stands

One of the two stands studied is located on Thatuna Ridge (referred to as the Thatuna stand) in Latah County, Idaho, and the other occurs along the Clearwater River in Nez Perce County. The Thatuna stand is at an elevation of 915 m and occupies the southwest-facing slope of a shallow ravine cut at a right angle to the low ridge which marks the western extremity of Thatuna Ridge. The average slope of the soil surface in the stand is approximately 10 per cent.

The soil, a gravelly silt loam, is residual and of granitic origin. There is possibly some admixture of aeolian material at the surface. It is well drained and porous with bed rock occurring from 0 to about 2 m below the surface. The proportion of sand and gravel particles (1 mm to 10 mm in diameter) increases with depth from less than 10 per cent at the surface to about 40 per cent in the C horizon.

The Clearwater stand is on the north-facing slope of the canyon formed by the Clearwater River. It is at an elevation of 247 m. The slope within the stand varies from about 10 per cent to 60 per cent.

The soil is colluvial and of basaltic origin mixed with recent aeolian material. The rather large basaltic fragments (10 mm to 200 mm in diameter) become relatively more numerous with an increase in depth. The soil matrix is a silt loam.

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[1] Taken from a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the State College of Washington, Pullman, Washington. This study was suggested by Dr. R. Daubenmire, whom the writer wishes to thank for help and advice.

The Thatuna stand belongs to the *Pinus ponderosa/Symphoricarpos rivularis* association and the Clearwater stand to the *Pinus ponderosa/Physocarpus malvaceus* association as described by Daubenmire (1952). Thus, the stand at the higher elevation occupies a habitat type more xeric than the stand at the lower elevation, as a result of microclimate more than offsetting the increase in moisture normally associated with increasing elevation.

No attempt was made to establish whether there is genetic uniformity between the trees in the two stands, but they lie a relatively short distance apart and are connected by intervening areas supporting this species, so that gene flow would seem unhampered.

Air temperature was recorded by means of two Sixe's maximum-minimum thermometers at each stand. The thermometers were placed in the shade about 4 feet above the soil surface. The air temperature was recorded as the maximum and minimum value attained between visits to the stands. While such data lack the refinement that might be desired, these are probably more reliable to compare temperature relations than are data from standard weather bureau stations, especially since the latter are located with the purpose of avoiding microclimatic influence.

Soil temperature was recorded at two depths during each visit using mercury-in-glass laboratory thermometers. One thermometer was placed at a depth of 1 m by inserting it into a metal pipe buried in a vertical position. The opening at the upper end of the pipe was kept stoppered. Soil temperature at a depth of 2 dm was recorded by placing the thermometer in a hole made with a steel rod. Examination of the temperature curves (Figs. 1 to 4) shows that in general the air and soil temperature values in the Clearwater stand are higher throughout the year than those in the Thatuna stand, in accord with the expected elevational difference.

Precipitation was collected by means of totalizer rain gages. The amount of precipitation was measured during each visit to the stands except when the moisture in the reservoirs was frozen; this occurred frequently during the winter at the Thatuna stand but rarely at the Clearwater stand. The gages were placed in the largest openings among the trees but it was not possible to place them at a distance greater than three times the height of the nearest tree; thus one is unable to draw conclusions based on the small precipitation differences measured because of unequal tree influence.

Phenologic data gathered for plants growing in association with the pines show that there is usually a two to three week difference in the time of leafing or flowering between the two stands, those in the Thatuna (colder) stand being the later.

Growth and phenology of the trees

Radial growth.—Radial growth measurements were made on 12 trees in each stand with a dial gage dendrometer (Daubenmire 1945). Two settings were installed approximately one foot above the base of each tree used, on different radii. The trees selected were in two size classes, 6 trees in each size class. Table I indicates the diameter at breast height and the number of growth rings of the trees used.

TABLE I. Diameter breast high and age for six trees per age class per stand

THATUNA STAND				CLEARWATER STAND			
Size class				Size class			
small		large		small		large	
d.b.h. (cm)	age*	d.b.h. (cm)	age*	d.b.h. (cm)	age*	d.b.h. (cm)	age*
8.1	29	86.4	71	10.7	18	53.3	72
11.9	29	58.4	68	7.1	23	61.0	70
7.9	22	71.1	69	7.6	20	66.0	70
14.0	38	63.5	70	10.1	21	50.8	75
7.6	30	58.4	63	10.7	39	48.3	78
7.1	30	68.6	71	13.0	43	58.4	78

*A value of 10 has been added to the breast height ages

During the first year of study visits were made to the Thatuna stand semiweekly until the end of the first summer, thereafter this stand was visited approximately once weekly. The Clearwater stand was visited weekly during the period of several months each year when the trees were physiologically most active; at other times this stand was visited fortnightly. On clear days during the summer, radial growth measurements were always completed by 8:30 a.m. to minimize the influence of transpiration draw-down. During the winter and on cloudy days during the summer, these measurements were frequently not completed until an hour or two later. No measurements were made when the air temperature was below freezing.

Apical growth.—Eight trees in each stand, 4 trees in each age class, were utilized in this study. Insect pins were inserted just proximally to the current year's growth in secondary and tertiary axes. The distance between the insect pin and the apex of the branch was measured with calipers to the nearest 0.5 mm. In all but two instances, the trees used for apical growth measurements were among those used for radial growth study. Two branches per tree were measured, usually a secondary axis and one of its subapical tertiaries. All branches measured were near the base of the tree so that no climbing was required to reach the branches. Measurements of apical growth were made on each visit to the stands during the season of active growth. Measurements were made less frequently at other times.

Needle growth.—Seasonal aspects of needle elongation were studied by determining the seasonal change in length of the needles in marked fascicles. On each of the branches chosen for use in the apical growth study, a single fascicle was marked with India ink. The fascicle selected was taken from the base of the needle-producing zone, for a wave of growth progresses from the base of this zone to its apex, each needle in turn commencing growth slightly earlier than the one next above. Calipers were used to measure the distance between the persistent base of the scale subtending the needle-bearing dwarf shoot and the apex of the needles. Measurements were made to the nearest 0.5 mm. If the needles in a single fascicle were of different lengths, an average value was recorded. This difference, however, was never great.

In the Thatuna stand, so many branch apices were killed during the course of the growing season by forces not accurately determined (probably insect larvae), that only 5 fascicles in 1952 and 9 fascicles in 1953 of those marked at the beginning of the season were living at the end of the season. Only those measurements from needles that survived the growing season were used in constructing the growth curves. Because of the small sample resulting from this damage the data for the two tree size classes were composited in this stand.

Table II shows the total average increments of all the vegetative features measured as well as the standard error of those means.

Needle abscission.—Seasonal aspects of the abscission of needle-bearing shoots were determined by placing beneath a single tree of each age class per stand, two (Thatuna) or three (Clearwater) needle traps. The dimensions of the wooden frames used as traps were 44.5 cm x 44.5 cm x 6.5 cm. The number of needle fascicles falling into the traps between visits was determined.

Pollen shedding period.—The duration and peak of the pollen shedding period was determined by collecting atmospheric pollen. Microscope slides, coated with a mixture of glycerine jelly, phenol, and safranin, were inserted within horizontally placed tinned cans from which both ends had been removed. A hardware cloth shelf was attached in the center of the longitudinal axis and across the horizontal diameter of each can. Upon this shelf, the slides were attached by means of a spring-type clothespin. The cans were approximately 11.5 cm long with a diameter of 11.0 cm. The cans were installed in pairs, two pairs per stand. The two pollen collecting stations in a stand were established on opposite sides of the group of trees under study. The two cans at a station were nailed to a tree at breast height, so that the longitudinal axes of the two cans were at right angles to each other. Exposed microscope slides were replaced by unexposed ones during each visit beginning slightly before and continuing until about two months after the peak of the pollen shedding season. It was usually necessary to drive off the moisture which condensed on the glycerine jelly by using an alcohol lamp carried for this purpose.

A coverslip (22 mm square) was placed on

TABLE II. Standard error of means and means of total annual growth increments for branch apices, stem radii, and needles

	BRANCH (mm)		STEM (mm)		NEEDLE (mm)	
	Tree size class		Tree size class		Tree size class	
	small	large	small	large	small	large
1952						
Thatuna..........	28.5± 3.5**	26.5±11.5**	2.29±0.30	2.82±0.28	121.5± 6.5†	184.5±37.5*
Clearwater........	89.5±17.0	43.5±12.0	3.89±0.48	3.51±0.28	147.5±10.0	183.0± 9.0
1953						
Thatuna..........	41.0±13.0‡	23.0± 7.0††	2.21±0.38	2.59±0.25	115.0±14.5‡	159.0±23.0**
Clearwater........	67.0±10.5	50.0±11.0††	3.73±0.48	3.63±0.25	156.0± 8.5	200.0± 9.5

*Sample composed of but 2 items
†Sample composed of but 3 items
**Sample composed of but 4 items
‡Sample composed of but 5 items
††Sample composed of but 6 items

the glycerine jelly and the area of the coverslip was then used as the sampling area from which the pollen counts were taken. The glycerine jelly was smeared on all of one surface of each slide except that portion at one end of the slide occupied by the slide label. The coverslip was placed near the center of this smear to minimize error due to border effect.

The technique used for mechanically sampling the area beneath the coverslip was as follows. An aluminum foil disc with a square orifice was placed in the ocular of the microscope. On low power each side of the field of vision defined by the square orifice equalled one division on the mechanical stage. Of 484 different squares included within the dimensions of the coverslip, 25 regularly spaced square areas were sampled, or about 5 per cent of the total was sampled. The number of pollen grains estimated to occur beneath the coverslip by using this sampling method agreed very closely with the actual number found when all pollen grains beneath the coverslip were counted. The error involved was 5 per cent or less on the several slides checked.

Growth of staminate cones.—The growth of staminate cones was followed by measuring the increase in length of tagged cones. These measurements were made only during the spring of that year in which the cones reached maturity although they completed a measurable increment of growth the previous autumn. In all instances, the number of cones used was probably insufficient, there being but one cone on each of two trees measured in the Clearwater stand in 1952. All other male cone data are based upon measurements of but 4 cones per stand.

Results

Radial growth

The results of the radial growth study show that the younger trees grew more rapidly than the older ones (Figs. 1 to 4). In the autumn, the young trees undergo wider radial fluctuations in response to changes in the moisture balance, as indicated by a comparison of precipitation data with the radial growth curves. Five per cent of total radial growth was accomplished about one to two and one-half weeks later in the Thatuna stand than in the Clearwater stand. The attainment of 95 per cent of total growth has little meaning here as a measure of the time of growth completion because the completion of this much growth may be masked by the shrinkage induced by dehydration during the late summer and fall so that there is considerable delay in reaching this point. This is especially true for the young trees which are apparently more responsive to changes in the moisture regime than the older trees.

The amount of autumnal shrinkage was greater in the Thatuna stand than in the Clearwater stand, a fact which is in agreement with interpretations of the relative dryness of *Pinus/Symphoricarpos* and *Pinus/Physocarpus* habitat types.

Apical growth

A comparison of the apical growth curves for the two size classes studied shows several noteworthy features (Figs. 1 to 4). The data from both stands show that growth in both age classes began simultaneously, but the younger trees grew at a slower rate at first and for this reason did not attain 5 per cent of their total growth until later than the faster growing large trees. By the time about 60 per cent or less of the annual apical growth had been attained, the percentage of growth for the younger trees surpassed that of the older ones. The general configuration of the curves for the two size classes is strikingly different, and the difference is consistent on both habitats and in both years of study. The older trees grew more rapidly at the branch apices for a much shorter period than the younger trees. The younger trees appeared to reach 95 per cent of the total annual increment before the older trees. Growth in length began two to three weeks earlier in the Clearwater stand than in the Thatuna stand, as was true of growth in diameter.

Apical growth began earlier than radial growth.

Needle elongation

The pattern of needle growth is distinctive when compared with the other growth features just described. In the Clearwater stand, the older trees began needle growth earlier than the smaller trees if one uses the attainment of 5 per cent of total yearly growth as the measure of time of growth initiation. The needles of the older trees appeared to maintain a growth lead throughout most of the growth period. The elongation of the needles began about two weeks later in the Thatuna stand than in the Clearwater stand.

At both stations, the total growth for the season was completed in about 90 days, a period of growth shorter than that for apical growth and apparently shorter than the ill-defined growth period for the stem radius.

Needle fall

The peak of the needle shedding period was somewhat more marked in the Thatuna stand and especially for 1952 (Figs. 1 to 4). In both stands studied, the peak came in September or October,

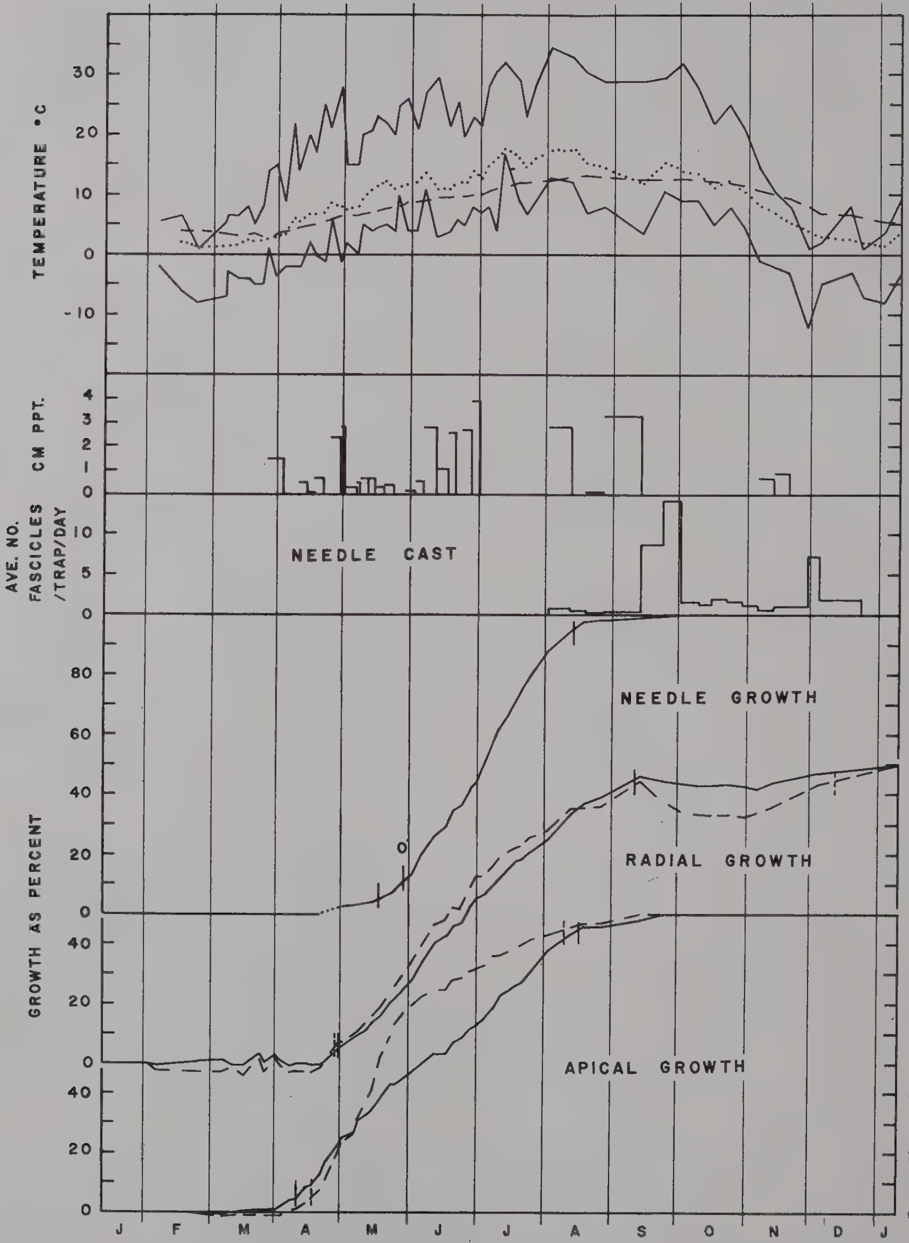


Fig. 1. Environmental and phenologic records for Thatuna Stand, 1952. Temperature: maximal and minimal air temperatures (solid lines), and soil temperatures at 20 cm (dotted line) and 1 m (dashed line). Precipitation: vertical lines indicate quantity, horizontal lines indicate length of the interval between measurements during which precipitation fell. Growth: curves show cumulative percentages of total yearly increment, dashed lines show growth for young trees, solid lines show growth for old trees. Short vertical lines intersecting growth curves show approximate date of attainment of 5% and 95% of total yearly increment. The vertical line marked 0 shows the approximate date of opening of the needle sheaths.

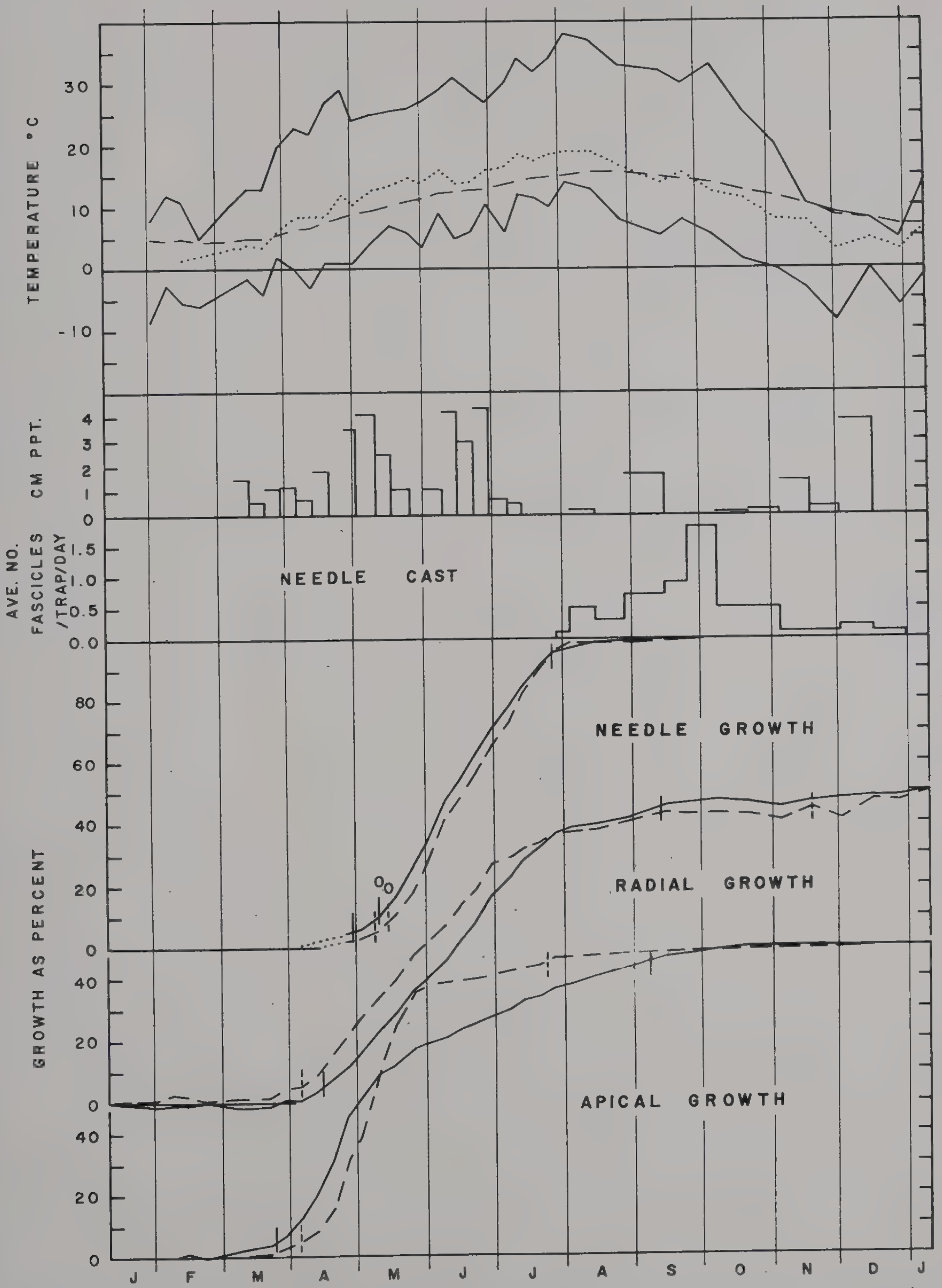


FIG. 2. Environmental and phenologic records for Clearwater Stand, 1952. Temperature: maximal and minimal air temperatures (solid lines), and soil temperatures at 20 cm (dotted line) and 1 m (dashed line). Precipitation: vertical lines indicate quantity, horizontal lines indicate length of the interval between measurements during which precipitation fell. Growth: curves show cumulative percentages of total yearly increment, dashed lines show growth for young trees, solid lines show growth for old trees. Short vertical lines intersecting growth curves show approximate date of attainment of 5% and 95% of total yearly increment. The vertical lines marked 0 show the approximate date of opening of the needle sheaths.

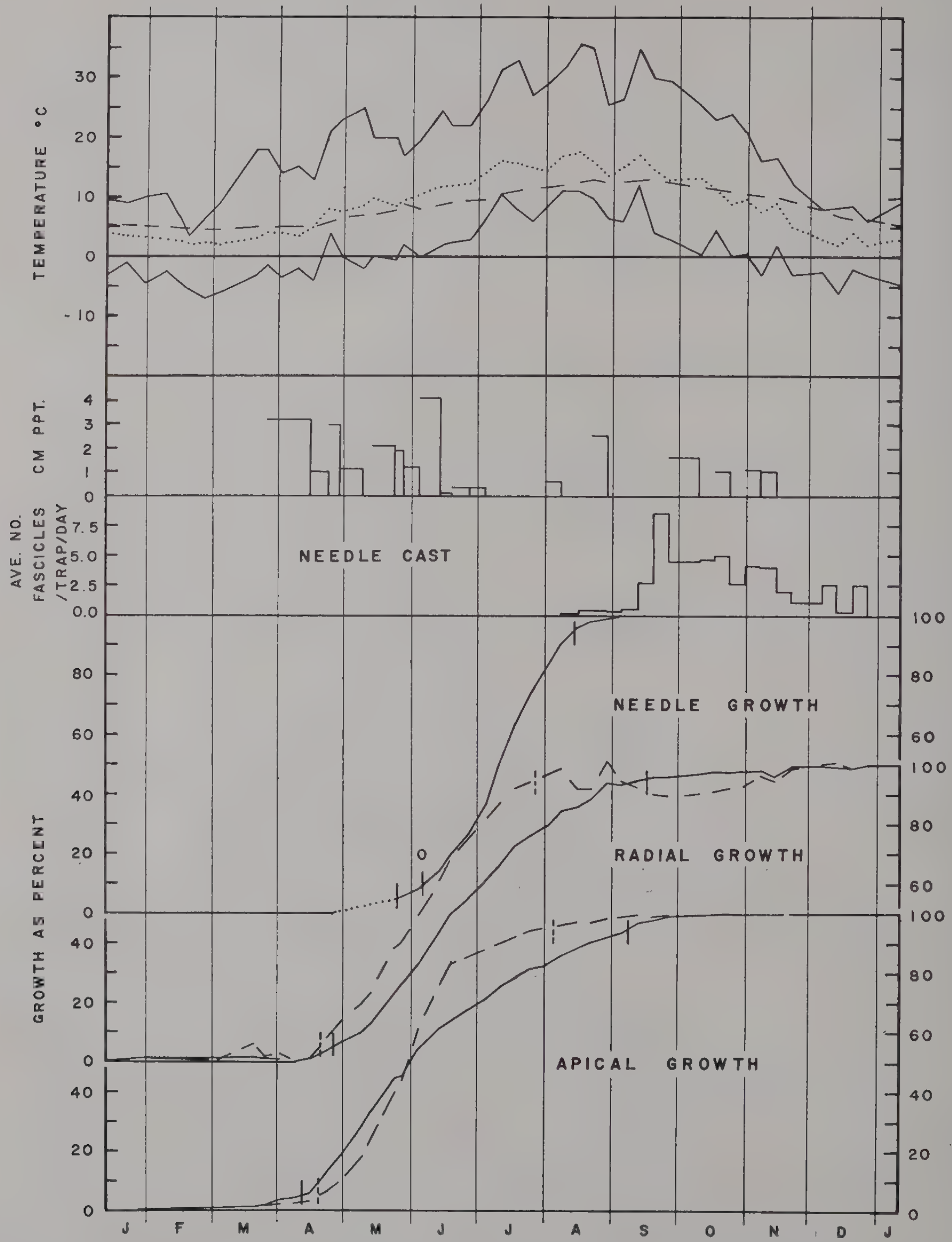


FIG. 3. Environmental and phenologic records for Thatuna Stand, 1953. Temperature: maximal and minimal air temperatures (solid lines), and soil temperatures at 20 cm (dotted line) and 1 m (dashed line). Precipitation: vertical lines indicate quantity, horizontal lines indicate length of the interval between measurements during which precipitation fell. Growth: curves show cumulative percentages of total yearly increment, dashed lines show growth for young trees, solid lines show growth for old trees. Short vertical lines intersecting growth curves show approximate date of attainment of 5% and 95% of total yearly increment. The vertical line marked 0 shows the approximate date of opening of the needle sheaths.

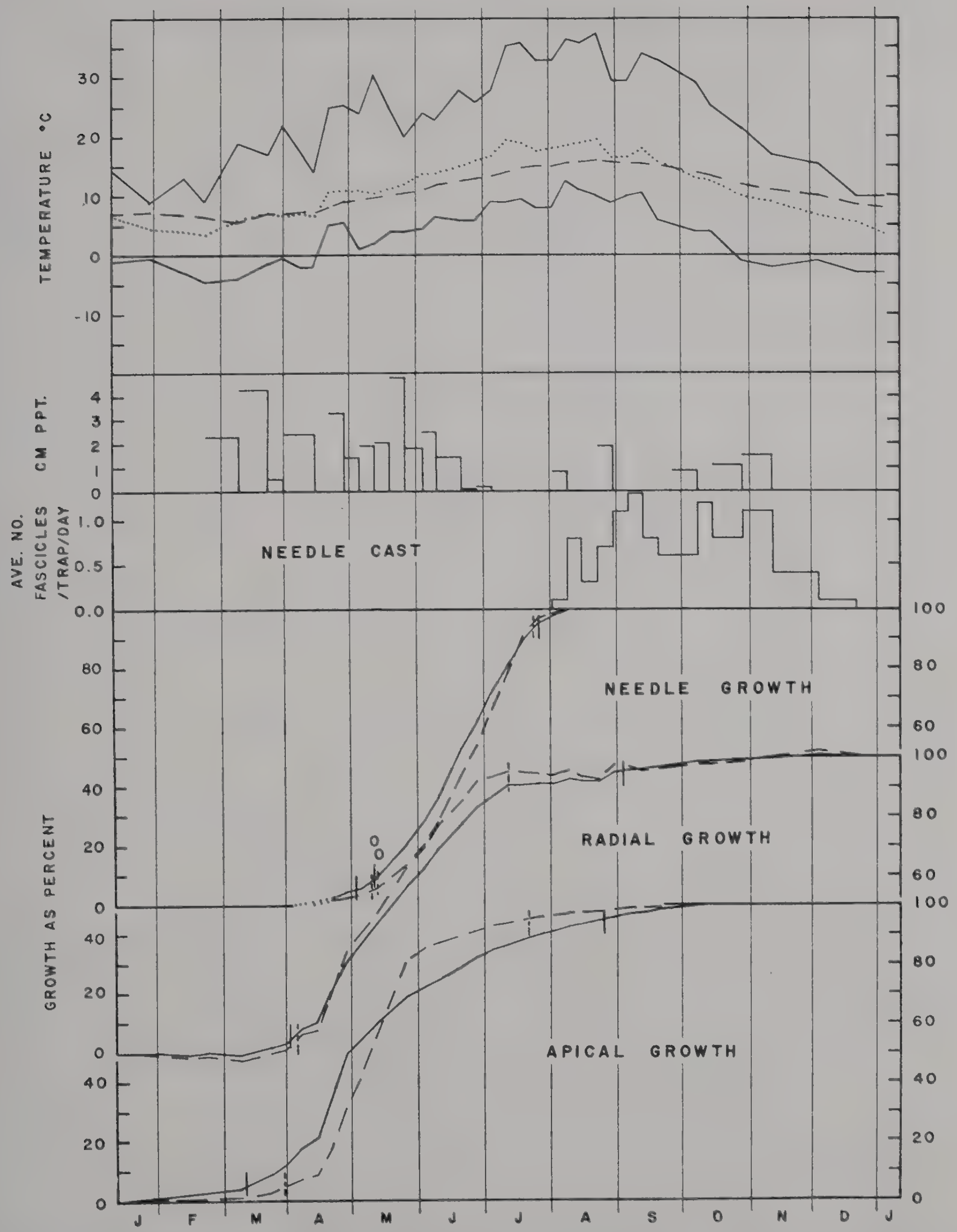
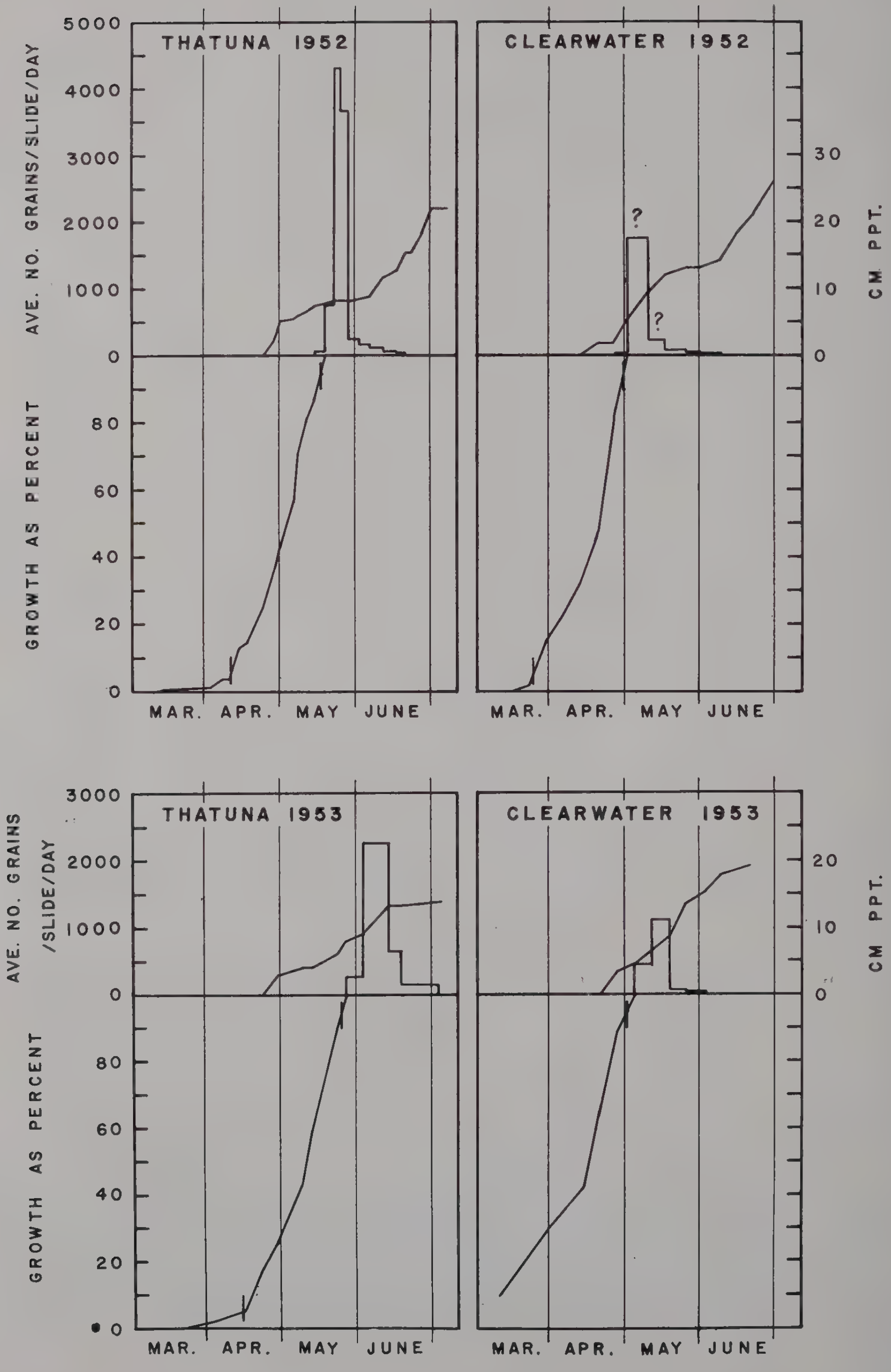


FIG. 4. Environmental and phenologic records for Clearwater Stand, 1953. Temperature: maximal and minimal air temperatures (solid lines), and soil temperatures at 20 cm (dotted line) and 1 m (dashed line). Precipitation: vertical lines indicate quantity, horizontal lines indicate length of the interval between measurements during which precipitation fell. Growth: curves show cumulative percentages of total yearly increment, dashed lines show growth for young trees, solid lines show growth for old trees. Short vertical lines intersecting growth curves show approximate date of attainment of 5% and 95% of total yearly increment. The vertical lines marked 0 show the approximate date of opening of the needle sheaths.


THATUNA 1952
CLEARWATER 1952
THATUNA 1953
CLEARWATER 1953
AVE. NO. GRAINS/SLIDE/DAY
AVE. NO. GRAINS /SLIDE/DAY
GROWTH AS PERCENT
CM. PPT.
5000
4000
3000
2000
1000
0
80
60
40
20
0
30
20
10
0
?
?
MAR.
APR.
MAY
JUNE

after the growth of the previously mentioned vegetative structures had ceased or was almost complete. The abscission of needle fascicles occurred within the period during the autumn when the radius of the stems decreased because of inadequate moisture. There may possibly be a physiologic basis for the apparent correlation between relatively small radial shrinkage of the trees in the Clearwater stand and the more prolonged period of needle cast at this stand.

Differences in wind intensity in the two stands may influence the needle-fall pattern. Many fasicicles, after abscission, become lodged among the branches of the tree, only to be dislodged later by a brisk wind. On several occasions in late winter following periods of strong winds, the surface of a fresh ground cover of snow has been seen heavily blanketed with such needles. The second sharp peak in the needle-fall histogram for Thatuna, 1952 (Fig. 1), is believed to be a result of fascicles being dislodged by strong winds from positions where they found temporary lodgement following abscission.

No attempt has been made to keep separate the needle-fall data for the two age classes of trees, since it was not possible to exclude needles from nearby large trees from the traps placed beneath the small trees and vice versa.

Staminate cone growth

Male cones exhibited a short growing season, rapid increase in length occurring within a 4 to 6 week period (Fig. 5). The opening of the male cone bud scales was preceded by relatively little elongation during the current spring although the cones had begun growth within the bud scales the preceding fall. In the Thatuna stand, for which the data are more complete, the male cones emerged through the parting bud scales at approximately the time when 5 per cent of the total growth for the cones had been attained.

In the fall of 1952, many of the male cones in both stands began growth as usual but exceeded the length of the bud scales. The cone buds remained in this opened condition throughout the winter but were apparently uninjured, for in the spring of 1953 germination tests of mature pollen were equally positive, both from cones which had been exposed during the preceding winter and from cones which had emerged during the current spring in the Clearwater stand. There was no consistent difference in the size frequency of the pollen produced by the two types of cones, although the air sacs were poorly developed in one of the two collections of pollen from exposed cones examined.

The season of male cone growth in the Clearwater stand preceded that in the Thatuna stand by about 3 weeks. The growth of the male cones came to a rather abrupt termination at which time the pollen was shed. The beginning of growth of the males cones corresponded rather closely to the beginning of apical growth in the vegetative branches.

Pollen shedding period

The pollen shedding period was consistently about 3 weeks earlier in the Clearwater stand than in the Thatuna stand (Fig. 5). The peak of the period coincided with a rainy period in both stands each year except at the Thatuna stand in 1952. Cumulative precipitation curves have been superimposed on the pollen-cast histograms to allow easier comparision. A comparison of the amount of pollen which fell during the 1952 rainless period and that which was collected when rains fell during the pollinating season emphasizes the important effect precipitation may have in curtailing pollination of this tree.

The early opening of certain staminate cone buds during the fall of 1952 did not result in an earlier ripening of these cones the subsequent spring. The peak of the pollen-shedding period in 1953 occurred more than one week later than the 1952 peak in the Thatuna stand, but at the Clearwater stand the peak for 1953 was no earlier and may have been later than for 1952. The period of maximum pollen shed in 1952 at the Clearwater stand was not closely identified since the slides exposed during the critical period became overheated during their transport to the laboratory, causing the glycerine jelly to liquefy so that much of it ran off the slides. The number of pollen grains remaining within the usual sampling area of the slides was determined so that the values arrived at are no more than an expression of the minimum number of grains known to be present. The question marks above portions of the histogram representing pollen shedding for the Clearwater stand, 1952 (Fig. 5), indicate the time intervals to which this limitation applies.

Inspection of Fig. 5 shows that the amount of atmospheric pollen increased relatively rapidly to a peak which was followed by a rapid decline and

FIG. 5. Atmospheric pollen and staminate cone growth records. Histograms indicate quantities of atmospheric pollen intercepted by traps. Superimposed on histograms are cumulative precipitation curves. Growth curves show staminate cone growth as cumulative percentages of total length. Short vertical lines intersecting growth curves show approximate date of attainment of 5% and 95% of total length.

then a long period during which the quantity of pollen in the air slowly decreased.

Discussion

In this study, it was found that cambial growth began earlier at the lower stand than at the higher one, which is probably related to the earlier onset of warm weather at the lower stand. The temperature difference can be most easily seen by comparing the date at which the soil temperature curve for 1 m depth exceeds some value such as 10° C. Temperatures from such a depth are especially useful because there is little diurnal variation in the values. The 10° C level is reached about 6 weeks earlier in the Clearwater stand than in the Thatuna stand. The difference in the time of cambial growth initiation of trees in the two stands suggests that day length exerts no decisive influence upon the initiation of cambial growth in this tree (assuming lack of genetic differentiation between the two stands). Additional evidence to support this hypothesis is the observation that the beginning of cambial growth differed rather widely within the same stand when comparing two years. This conclusion as to lack of photoperiodism is in agreement with other studies concerned with cambial growth in this species.

Fowells (1941), for example, found that radial growth of ponderosa pine commenced at a significantly later date with an increase in elevation of 2000 feet. No temperature records were presented, but the differences in growth pattern at different elevations are presumably a result of the temperature gradient.

Two studies by Daubenmire (1949, 1950) substantiate this view. It was shown (1949) that over a period of three successive years the date of beginning of rapid enlargement of the stems of several individuals of this species varied by 17 days. In the 1950 study of different geographic races of this species growing in the same habitat, it was shown that there is no correlation between geographic origin and the date of cambial growth initiation. Therefore, it was concluded that day length does not determine the beginning of cambial activity. Since soil moisture is not limiting during the spring it appears that under the conditions of the above studies, temperature is the environmental requirement with which cambial growth initiation is most closely related.

It has been shown previously in studies conducted by others (Fowells 1941, Daubenmire 1946) that with increasing elevation along a mountain slope the amount of autumnal shrinkage in ponderosa pine decreases. In the present study, the opposite relationship was found for there was less autumnal shrinkage in the lower stand than in the higher one. These results are not inconsistent with those of the previous workers for the usual altitude-moisture relationship has been reversed; the lower stand belongs to the plant association with the better moisture balance in which one might expect less shrinkage, since shrinkage is due to dehydration of the cells of the trees during periods of moisture stress. This emphasizes the importance of the ecologic position of the trees rather than their relationship to some non-biologic feature such as altitude.

McMinn (1952) found that in stands of the *Pinus/Physocarpus* association soil drouth developed later in autumn than in stands of the *Pinus/Symphoricarpos* association. The results of McMinn's study, which was conducted in the same general area as the present study, make more tenable an hypothesis that the lesser amount of radial shrinkage in the *Pinus/Physocarpus* association is related to a better moisture balance in that association.

Early European workers believed that initiation of cambial growth proceeds through the main axis of the tree from above downward, the impulse proceeding from developing buds. The work of Avery, *et al.* (1937) and Fraser (1952) strongly substantiates this view. Also, Friesner and Walden (1946) found that, in *Pinus strobus*, initiation of radial growth follows closely the swelling of terminal buds. The finding in the present study that radial growth initiation followed the beginning of elongation of basal branches agrees with this theory provided the beginning of elongation of the leader and of secondary and tertiary axes is closely synchronized. Evidence for this synchronization was found in a study of two ponderosa pine saplings. During two growing seasons, there was no detectable difference in the time that growth of the leaders and secondary axes began. Radial growth measurements were not made on the two small trees used for this study of synchrony. In other pines, also, the commencement of height growth and of the growth of secondary and tertiary axes closely coincide. Thus, Friesner (1943) found that elongation begins in primary, secondary, and tertiary axes of *P. strobus* and *P. resinosa* at the same time regardless of position in the contour of the tree.

The findings of Fowells on *P. ponderosa* (also *P. lambertiana, Libocedrus decurrens,* and *Abies concolor*) in the Sierra Nevada are not in agreement with the theory of the apical origin of stimulus since the beginning of height growth was found to follow radial growth initiation. Fowells' conclusion may be questioned, however, since the trees used for leader growth measurements were considerably younger than those trees used for radial growth measurements.

The present study (see also MacDougal 1924: 46) shows that when following growth features of ponderosa pine, at least, one should keep distinct the various age classes. The younger trees are probably responding to a slightly different set of environmental conditions (because of differences in extent of exposure to atmospheric factors, extent of root system, thickness of cork, etc.), and, indeed, might be expected to respond in a slightly different manner to the same set of environmental conditions since they are physiologically immature.

The early rather abrupt termination of rapid apical growth may be the result of internal competition. Since elaborated foods, water, and minerals will be drawn to each growing region, there is probably severe competion within the plant for these growth materials. The increased activity of a growing region may increase the attraction it has for these growth materials, and if the supply is limited, other growing regions may gradually cease their activity because the availability of these substances is decreased. Such a relationship may exist between the needles and the branch apices. The onset of growth in the needles is probably accompanied by a diversion of essential growth materials from the growing branch apex so that growth of the latter is greatly restricted. The close proximity of these two growth regions would serve to accentuate the competition since the route followed by the growth materials to reach these two regions would be the same.

SUMMARY

A quantitative study was made of some features of growth in two age classes of *Pinus ponderosa* Laws. at two elevations in northern Idaho. The elevations of the stands differed by about 670 m. The higher of the two stands selected belongs to the *Pinus ponderosa/Symphoricarpos rivularis* association and the lower stand belongs to the *Pinus ponderosa/Physocarpus malvaceus* association, but the usual altitudinal sequence of these associations is reversed, for owing to microclimatic compensation, the association with the better moisture balance occurs at the lower elevation.

The commencement of growth of all structures studied was earlier in the lower stand, presumably because of the earlier onset of warm spring weather in that stand.

The patterns of growth of the branches, stems and needles were different. This growth pattern also differed in a characteristic manner between the two size classes of trees.

Elongation of branch apices and staminate cones begins first, followed by radial growth of the stem, and finally needle elongation. The male cones complete their development and the pollen is shed shortly after needle elongation commences. Needle fall occurs in autumn after the other structures studied have completed essentially all their annual growth increment, and coincides with shrinkage of the stem diameter.

Autumnal shrinkage of stem radii was not so severe in the lower stand as in the upper stand, presumably because of a better moisture balance in this more moist stand.

The younger trees appeared to respond more to changes in the moisture balance than the older trees during the period of autumn drought.

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A REVIEW OF THE GENERAL LAND OFFICE SURVEY AND OF ITS USE IN QUANTITATIVE STUDIES OF FORMER FORESTS[1]

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Introduction

Forest and prairie, as the first settlers found them, have been almost completely destroyed by the advance of civilization. During the past several decades, however, there has been considerable effort in some states to reconstruct the general characteristics and distribution of the vegetation our pioneering forefathers saw. Contemporary field studies provided much (or even all) of the data on which some vegetation maps are based. Yet second-growth stands and scattered old-growth remnants cannot, without great hazard, be used alone to delineate original vegetation, much less to provide reliable information on its composition. Disturbed tracts usually are radically altered from their former character, while remnants often represent subclimax types in which man's protection may have induced equally great change. Interpolation between isolated tracts is difficult, generally unsatisfactory, or even impossible. Therefore, information from the past ordinarily is required to tie present stands with those which existed earlier and to fill in the gaps.

The sources of this information are relatively few. Bromley (1935) lists three kinds of prehistoric evidence, including fossil pollen, and four kinds of historic evidence. Of the latter, land surveyor's records have been most commonly used. Old survey records are available for most of the continental United States. They possess the special advantage of having been written on the spot according to a previously determined plan. Moreover, they constitute a definite sample of the vegetation; thus, they are usable for quantitative as well as qualitative analyses. Practically all workers referred to the rectangular surveys of the General Land Office, although even metes and bounds surveys of colonial states can throw light on contemporary vegetation (Spurr 1951). Rectangular surveys privately contracted on a similar plan have also been used (Lutz 1930, Gordon 1940).

In general, investigators have sought two kinds of information from the surveys. Some have concerned themselves only with qualitative data from which to construct maps showing the distribution of forest types within counties, or larger units (Davis 1907, Kenoyer 1929, *et seq.,* Marschner 1946, as redrawn by A. D. Perejda). Other people (Cottam 1949, Brown 1950) have been specially concerned with the spatial arrangement and size class distribution of trees within timber types. They used the species and the diameters of the trees recorded, as well as their distance and direction from the corner post, or from each other, to obtain quantitative information on the composition and structure of forest types. Many workers combined both approaches, sometimes by reference to survey notes alone, but more often in conjunction with other data.

Writers commonly have justified their use of survey data (Sears 1925, Kenoyer 1929, Shanks 1937). Some have even compared "virgin" remnants with reconstructions based on surveyor's notes (Lutz 1930, Stearns 1949, Blewett and Potzger 1950), but the stands involved were small. An effort at broad review of the original survey and of its use in reconstructing original vegetation is timely, especially in view of the amount of work that has already been done. Major emphasis will be placed on those quantitative (and qualitative) inductions for which the survey usually represents the sole source of information.

Four tracts of land in the western part of the Upper Peninsula of Michigan provide the basis for comparisons in this paper. For ease of reference, they have been named the Misery Bay Block, the Alberta Block, the Huron Block, and the Keweenaw Point (Fig. 1). The townships selected have a combined area equal to that of a small county, but few counties in the Central States possess such great variety of topography, soils, and geological formation (Leverett 1917, 1929, Veatch 1953, Van Hise and Leith 1911). At the time they were studied, uncut timber and stands which had been partially (selectively) cut within the last 15 years constituted a large part of the cover on them—over half in the cases of the Keweenaw and Huron blocks.

As a result of the Forest Survey, excellent information on the constitution and distribution of forests is available for the whole Upper Peninsula (Cunningham and White 1941), for the western part of the Peninsula (Cunningham and Moser 1939), and for Marquette and Baraga counties (Chase 1947, Chase and Horn 1951). The actual distribtuion of timber in the blocks was de-

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[1] Portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Michigan, Ann Arbor, Michigan.

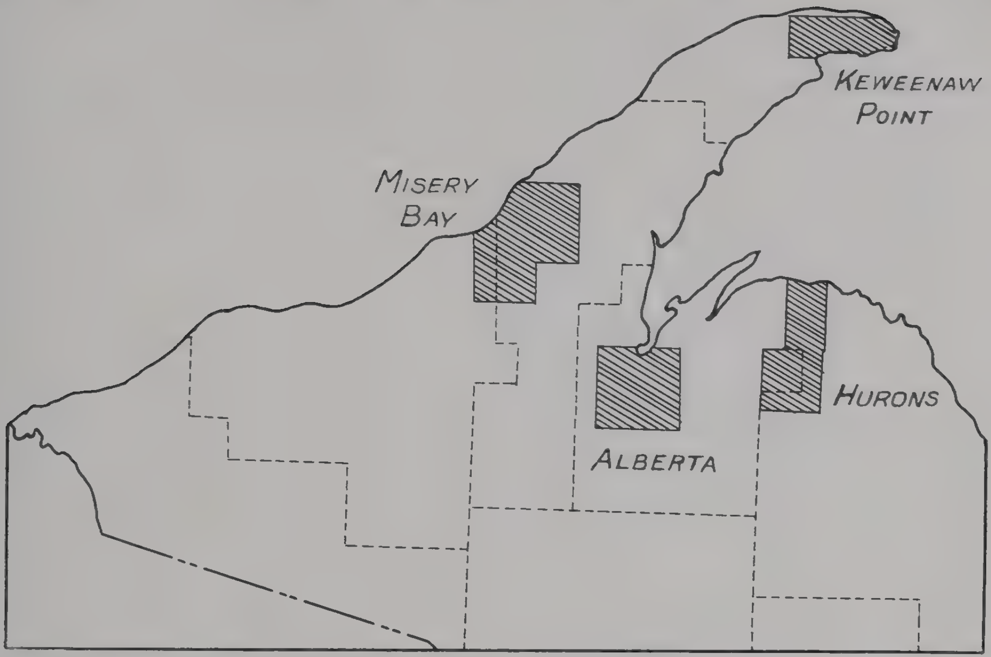

FIG. 1. Western portion of the Upper Peninsula of Michigan showing the location of the areas studied.

termined from recent aerial photographs, however. In general, the types mentioned in this paper conform most closely to the Lake States Cover Types (as listed in the Appendix of the Forest Survey Section of the Timber Management Handbook for Region 9), which themselves are adaptations of those recognized by the Committee on Forest Types of the Society of American Foresters (1940). Integration with Lake States types (Table I) made possible the use of Forest Service data. In vegetation reconstructions from the original land survey, it is impossible to distinguish some of the associations listed in Table I; therefore, field data for the appropriate types were combined when comparison with a broader category (such as northern hardwoods) was desired.

TABLE I. Correlation of forest types recognized in the areas studied with Lake States and Society of American Foresters cover types

Type and symbol	Lake States type	S. A. F. type
Northern hardwoods	M	
Sugar maple (M)	—	14
Yellow birch (B)	—	15
Sugar maple-yellow birch (MB)	—	12
Mixed hardwood* (MX)	—	—
Hardwood-hemlock† (MH)	—	—
Mixed swamp hardwoods (SX)	Ms	26
Hemlock (H)	H	11
Black spruce (S)	7	23
White cedar (C)	4	24
Spruce-fir (SF)	6	21
Aspen-paper birch (A)	A	4 & 6
Jack pine (J)	5	1
Red pine (N)	8	2
White pine (P)	9	9

*Mixed upland hardwoods. No species predominant
†Hemlock representing 25 to 50 per cent of timber volume

Northern hardwoods predominate in the study blocks, but hemlock, spruce-fir, jack pine, and other northern types are well represented. The Misery Bay Block consists almost entirely of northern hardwoods and hemlock stands, major boundaries conforming largely with former beaches of glacial great lakes. Similar stands have been discussed by others (Whitford 1901, Darlington 1930, Graham 1941). A sugar maple sub-type occupies moraine which the lakes never covered, hardwood and hardwood-hemlock sub-types dominate the beds of Lake Duluth and Lake Algonquin, while extensive stands of hemlock also covered portions of the bed of the latter lake. The Alberta Block is similar, but hemlock is more generally distributed and a portion of the sandy Baraga jack pine plains is included. Hemlock is absent from the greater part of the other two blocks, but spruce and fir are widely distributed. The hardwood timber is much interrupted, especially on the higher land, by rocky outcrops, small and large bogs, wet sedge meadows, and local old burns or blowdowns. Because of its homogeneity, the Misery Bay Block was particularly well adapted for comparisons involving northern hardwoods.

For direct comparison with survey information, one-twentieth acre circular plots were taken at 152 section and quarter corners. At 49 of these corners, one or more bearing trees were still standing. At every plot, the species and d.b.h. (diameter breast high) of every tree were tallied, as well as the course and direction of each from the corner post. Basal area was determined with an angle-count cruiser's stick (Grossenbaugh 1952). Approximately 400 auxiliary plots, mostly in old-growth timber, provided supporting data. Timber estimates, timber marking records, and cutting tallies were available for thousands of acres within the study blocks, while notes on over 400 corners visited during the past 8 years furnished additional information.

The northern hardwoods type is particularly well suited to provide quantitative comparisons between past and present vegetation because of its density, the wide distribution of diameter classes in it, and the relatively small number and long life of the dominant species which compose it. It seems safe to assume that so long as large areas of uncut northern hardwoods are considered, important *net* change has not occurred in the last hundred years either in the general distribution of the type and its subtypes, or in their average composition. The hemlock type is equally stable. Growth and death of individual trees will have caused more or less modification in stands, of course, and some may have been altered radically by windthrow and local fires. Although there may also have been some change along a continuum gradient (Stearns 1949, Brown 1952), the area occupied by each recognized association will be essentially the same. This is true largely because the predominant species are very long-lived (Eyre and Zillgitt 1953), and in the relatively short period of a century, they are capable of maintaining their representation.

Data from the 1936 Forest Survey (condensed from Eyre and Zillgitt 1953: 28-29) provides the best available "standard" for northern hardwoods in the area (Table II). Cull trees in the table are all hardwoods, but are not otherwise identified. Although based on a much more limited sample, the distribution at corner plots in northern hardwoods does not differ significantly from this "standard," and both sources were used for comparison with information from the original survey.

TABLE II. Stand and basal area table for old-growth northern hardwoods in the western half of the Upper Peninsula of Michigan (Condensed from Eyre and Zillgitt 1953: 28-29)

Diameter class	Sugar maple	Yellow birch	Hem-lock	Others*	Cull trees†	Total trees	Basal area
2	68.39	7.76	12.83	50.94	1.37	141.39	3.11
4	21.67	4.79	10.25	23.48	1.65	61.84	5.38
6	8.92	3.08	7.20	12.00	1.79	32.99	6.47
8	6.64	2.55	5.74	8.28	1.58	24.79	8.65
10	5.55	2.27	4.63	5.13	1.45	19.03	10.37
12	5.43	2.22	4.05	2.99	1.29	15.98	12.54
14	4.82	1.90	3.12	2.08	1.02	12.94	13.83
16	4.38	1.92	2.69	1.58	.85	11.42	15.95
18	3.47	1.48	2.18	0.96	.84	8.93	15.78
20	3.25	1.26	1.95	0.66	.60	7.72	16.85
22	1.50	0.87	1.54	0.39	.49	4.79	12.64
24	0.80	0.66	1.19	0.23	.40	3.28	10.31
26	0.42	0.45	0.80	0.13	.22	2.02	7.45
28	0.19	0.27	0.44	0.10	.13	1.13	4.84
30	0.06	0.16	0.36	0.06	.13	0.77	3.78
32	0.03	0.09	0.15	0.04	.05	0.36	2.01
34	....	0.05	0.11	0.02	.04	0.22	1.39
36	....	....	0.02	....	.02	0.04	0.28
38	....	....	0.01	0.02	.01	0.04	0.32
40	....	....	....	....	.01	0.01	0.09
42	....	....	0.01	....	....	0.01	0.10
Total	135.52	31.78	59.37	109.09	13.94	349.70	152.14

*Includes red maple, black ash, ironwood, black cherry, white ash, paper birch, balsam fir, white spruce, northern white cedar, and white pine

†Not identified, but all hardwoods

Copies of the surveyor's notes on file at the courthouses of Houghton, Keweenaw, Baraga, Ontonagon, Marquette, and Iron counties were examined, and transcripts were made of those portions pertaining to the study blocks. Town and range line surveys were kept separate from the subdivision surveys for reasons that will appear later. Trees at meander and witness corners were not included in either count; nevertheless, almost 4,000 bearing trees and over 5,000 line trees were available. The surveyor's notes for a number of counties in the Lower Peninsula of Michigan also were inspected cursorily, and data for townships in Muskegon, Newaygo, and Ingham counties were taken to provide some comparisons. Recent resurveys also allowed comparisons between new bearing trees and the old ones.

The correlation of surveyor's names for trees with those in use today was made easy by the existence of two early lists (Burt and Cooley 1849, Foster and Whitney 1851). In old-growth stands, the dominant hardwood bearing trees and line trees were sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), red maple (*Acer rubrum*), and basswood (*Tilia americana*). Of lesser importance were ironwood (*Ostrya virginiana*), white and black ashes (*Fraxinus americana* and *F. nigra*), elm (mostly *Ulmus americana*, but probably some *U. rubra*), and red oak

(*Quercus rubra*). Beech does not occur in the western portion of the Upper Peninsula. Hemlock (*Tsuga canadensis*), spruce (*Picea glauca* and *P. mariana*), fir (*Abies balsamea*), jack pine (*Pinus banksiana*), and cedar (*Thuja occidentalis*) were the chief coniferous species, although larch (*Larix laricina*), white pine (*Pinus strobus*), and red pine (*Pinus resinosa*) also were reported. Pioneer hardwoods, especially aspen (*Populus tremuloides* and *P. grandidentata*) and white birch (*Betula papyrifera*), were common in some townships.

Review of Surveyor's Instructions

The techniques of land subdivision are today well standardized, but a large proportion of the public domain was surveyed while these techniques were being evolved. The specifications, therefore, changed from time to time. The major changes were embodied in general instructions issued at intervals by the Surveyors-General of the United States. Ordinarily, it can be assumed that a given survey conformed to the instructions in force at the time that survey was made, although special orders accompanied each contract and these often were augmented by letter. Moreover, it was possible for a deputy-surveyor to introduce in the field innovations to improve the work. Dodds, *et al.* (1943, Chapter 3), have assembled the general instructions for 1815, 1831, 1834, 1843, 1845, 1850, 1851, and 1855. These cover most of the period in which people working on vegetation reconstructions are interested. Only a small part of the public domain was subdivided before 1815, while as the authors put it (page 115): "The instructions of 1855 . . . were the guide book for practically all surveys from that time until the end of the contract system in 1910." The authors further emphasize that: "For those surveys completed before 1855 it is very important to compare the survey record as preserved in the original plats and field notes with the current original instructions of the same date as the survey."

Inspection of the literature suggests that most workers were not aware of the particular instructions which applied to the areas each investigated. Citations of surveying techniques are few and usually refer to standard handbooks (such as Davis and Foote 1953), which detail present procedure while only briefly mentioning historical development. The importance of full knowledge concerning the conduct of early surveys varies, of course, with the kind of vegetation study being made and the proportion of the data which the survey notes supply. Those early procedures which bear most heavily on the interpretations that are attempted today will be reviewed.

The rectangular system of surveying public lands was authorized by Congress with the Ordinance of May 20, 1785. It represented a radical departure from the custom of land subdivision by metes and bounds which prevailed in the colonies, although traces of earlier rectangular units have been found in colonial tracts (Assoc. Eng. Soc. 1908) and special surveys were made there later. Stewart (1935) reviewed the legislation adopted by Congress to establish the framework for conduct of the survey. The first tract partitioned under the Ordinance of 1785 was that now known as "The Old Seven Ranges" of southeastern Ohio. Townships were laid out, but were not subdivided in the field. The Act of May 18, 1786, provided for the subdivision of townships into blocks of 4 square miles by tracing alternate section lines. Section corners were set at mile intervals on these lines. Later laws required all section lines to be run and allowed for resurvey of previous work, so that with the Act of February 11, 1805, all the lines and corners we know today were specified.

The designations "bearing tree" and "witness tree" often are used interchangeably—indeed, most of the general instructions do not differentiate between them. The letters, "B. T." (bearing tree), were required in 1831; but only in 1846 and 1851 is the bearing tree defined as one to which both course and direction are taken and on which two blazes are placed, a large upper one to bear the corner identification and a small one near the ground for the letters, "B. T." Witness trees, on the other hand, are signalized and chopped like bearing trees, "but the course and distance to them is omitted as well as the small chop."

All instructions specify 4 bearing trees, both at township corners and at section corners on township and range lines. One of these trees was to stand in each of the 4 sections common to a corner. The usual practice was to set two trees when the townships were laid out and the others when the lines of subdivision were tied in. Frequently only two or three bearing trees actually were reported. Except in 1850, 4 trees were required at interior section corners as well. It is not clear, however, whether all of these were to be bearing trees. In 1855, for example, "courses (from the post) must be taken and distances measured to two or more adjacent trees in opposite directions, as nearly as may be, and these are called 'bearing trees.'" A similar injunction was given in 1815. In 1846, only two trees were designated as bearing trees, while the other two were called witness trees. In 1850, two or more bearing tress were required, but where a living tree could be used as a post, only "at least one bearing tree must be taken." Commonly, no more than two trees were reported at interior corners.

At all quarter corners, only two bearing trees were needed. In 1834, they were to be "two of the most suitable trees in two different quarter sections. . . ." In 1831 and 1850, they had to be the nearest *adjacent* trees in each section; in 1843, 1851, and 1855, they needed only to be in different sections. The above explains why in Muskegon County, Michigan, surveyed in 1837, the bearing trees at quarter corners are in adjacent quadrants as often as in opposite quadrants, while in those parts of Houghton County subdivided after 1850, the bearing trees are almost entirely in opposite quadrants.

In timbered country, the lines established by the surveyors inevitably intersected one or more trees. A double blaze was placed on all line trees (sometimes called station trees), one directly above the other. In 1850, the surveyor was instructed to record in his field notes "the names and estimated diameters of at least one or two of these trees . . . with their exact distances on the line, between every two corners." In 1843, the requirement was similar; but the instructions of other years stipulated that *all* trees which the line intersects must be recorded in the notes. In the latter instances, the line trees should be random selections, but it is difficult to assess the bias, if any, which might have occurred when the 1843 and 1850 instructions were followed. An inspection of the surveys for a number of Michigan counties indicates, however, that no more than two trees ordinarily were reported per half mile of line. In the Upper Peninsula, there was a conscious effort to select two trees (occasionally one) so that each half mile was segmented as evenly as possible.

The point on a bearing tree to which a measurement from the post was taken is not specified in any of the instructions. In 1850, however, bearing trees "shall be blazed near the ground with a large blaze facing towards the post, and have one notch neatly and plainly made with an ax, square across, and a little below the middle of the blaze." It was to the notch that the measurement actually was taken, even though this is not stated. The notch can usually be found on hardwood bearing trees which have not become butt-rotted. On burned pine stumps, the notch sometimes is the only evidence that survives the fire. In 1855, it was the upper of the two bearing tree blazes that was to be notched "at its lower end," but nothing is said about placing a similar cut on the lower blaze.

In any event, the measurement does not signify the distance to the center of the trees. Therefore, in computing mean distances of bearing trees from the corner posts, or in attempting to approximate basal areas from field notes, the radius of a tree should be added to its measured distance. The error introduced by failing to do so diminishes, of course, with decreasing tree size and as the average distance from the post increases. In scattered timber it is negligible, but in heavy growth the error may be appreciable. In stands of northern hardwoods, several samples indicate that figures at least 5 per cent high will be obtained if the adjustment is not made.

The diameter of a bearing tree was estimated —in fact, that still is the usual practice today in resurvey work. In general, diameters were reported in even inches, especially for the larger trees, although in some townships, uneven diameters constitute about half of the total. Certain large diameter classes (20 inch, 24 inch, 30 inch, and others) often were estimated with excessive frequency. Cain (unpublished), working in Ogemaw County, Michigan, has found that a curve could be drawn to smooth the clusters and that this curve approximated one representing stand table data for the type. Comparisons between actual stand tables and some drawn from survey records are presented later.

When a township was completed, the surveyor was required to draw a plat of it. There is considerable variation in the amount of detail which these plats show. Some in Keweenaw County present merely the length of section lines and the location of mining claims. Others were sufficiently detailed so that early regional and state maps were made directly from them (*e.g.*, John Farmer's maps of 1830, and later). Until recently, some county maps (*e.g.*, Baraga County) were little more than modified reproductions of the surveyor's plats. Many investigators have found tracings of township plats to be useful as a base for vegetation maps.

Certain other specifications of the survey deserve brief mention. Every major change of cover was to be reported and the chainage given. At the end of each mile (in 1834, each half mile), the timber and undergrowth was listed—in some cases, even the prominent herbaceous plants as well. When cover changed radically, the vegetation of each area was reported separately. From 1843 on, tree species were required to be named in the order of their prevalency. In 1850, it was further required to report in prairie localities, "the kind of grass or other herbage it produces." Finley (1951) made use of species sequence reports in constructing his vegetation map of Wisconsin.

The detail obtainable from survey data is well illustrated by the following paragraphs from the 1850 instructions (they were listed under the heading "Of Field Notes," by the item numbers used below):

24. "All rivers, creeks, and smaller streams of water, with their right-angled width, and the course they run where the lines of your survey intersect or cross them, and whether the current be rapid, sluggish, or otherwise."

27. "All lakes and ponds, with the description of banks surrounding them, and whether the water be deep or shallow, pure or stagnant."

29. "All prairies, swamps, and marshes."

30. "All coal banks or beds, and peat or turf grounds."

31. "'All precipices, caves, stone quarries, and ledges of rock, with the kind of stone found in them."

38. "The tracks of tornadoes, or hurricanes, commonly called 'windfall' or 'fallen timber,' showing the direction of the wind, as indicated by the fallen trees."

41. "At what distance you enter and at what distance you leave every lake, bay, pond, creek, bottom, windfall, grove, prairie, ravine, marsh and swamp, with the course of the same at both points of intersection; also the distance at which you begin to ascend, arrive at the top, begin to descend, and reach the bottom of all hills and ridges, with their course, and estimated heights in feet above the level land of the surrounding country, or above the bottom lands, ravines, or waters on which they are situated."

Many workers (Davis 1907, Sears 1925, Kenoyer 1929, *et seq.*) relied heavily on this kind of information. In any event, it permits the boundaries and character of vegetation types along section lines to be more closely demarcated than by dependence on bearing trees alone—in fact, without it small swamps, bogs, and bottoms can scarcely be mapped at all.

Fraud and Bias in the Survey

No data can be any better than the person who collected them. Instances of gross malpractice, like the frauds of the infamous Benson Syndicate in California, have caused people to doubt the utility of survey data for vegetation reconstructions. Stewart (1935) cites numerous instances of fraud, some of them in the Central States. He quotes Lucius Lyon, Surveyor-General for Ohio, Indiana, and Michigan, as reporting in 1849 that the returns for many townships were "grossly fraudulent—the greater portion of the field notes there being wholly fictitious, or descriptive of lines and corners that never were established." Lyon estimated that at least 150 townships in Michigan's Southern Peninsula would have to be resurveyed. Whether they were, is not stated. As Stewart points out, field examination of surveys did not really become effective until 1881. Before that time, examinations were conducted by the Surveyors-General themselves in their respective districts.

Even the most dedicated of deputy-surveyors was not safe from cheating by his men. William A. Burt, who invented the solar compass, whose work was of excellent quality, and whose integrity is beyond question, discovered that some men he hired to subdivide townships had turned in spurious records. He reported that in one township, insofar as it was examined, nearly half of the lines and quarter section corners described in the original field notes had never been established. Further examination revealed that in 7 other townships, less than one third of the lines and corners described in the field notes had any existence on the ground. Burt resurveyed these townships at his own expense. To have subdivided some townships in the time reported, a crew would have had to survey as fast as the men could walk. There are surveys on record where they must have moved even faster.

All cases of error are not due to premeditated fraud. Some simply are mistakes that were made inadvertently or through carelessness and either were not recognized at the time or were not corrected. Instances of slipshod work are not infrequent. Quarter corners on east-west lines are required to be set on a line which first is run random from one section corner to the corner one mile east, and then is corrected back. Some men tried to reduce the work by running the line only a half mile east, then setting the corner directly. This short cut makes dropped chainage (forgotten or "lost" count) difficult for them to discover; detection of the error might not occur until several miles of line were run. In these cases the work probably was not redone, which explains the large discrepancies sometimes found on interior lines. Many actual cases of poor line running could be cited. Figure 2 shows where the bearing trees were found for a series of corners in T54N-R36W, Houghton County, with respect to the places they were supposed to be.

Errors of this sort do not necessarily affect the usefulness of the field notes. I have visited many

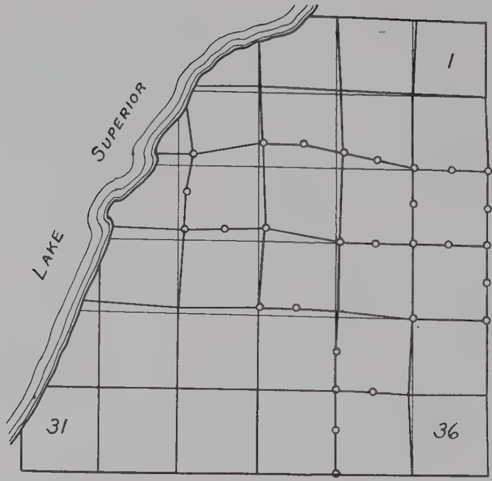

FIG. 2. Location of section lines and corners in T54N-R36W, Houghton County, according to lines resurveyed and bearing trees found by C. Lawrence, Registered Surveyor. Circles represent corners at which General Land Office bearing trees were found.

of the corners shown in Figure 2. They were located in heavy timber and nothing seemed to be wrong with the way in which they were set, no matter how poorly the lines were run. There is, in fact, reason to believe that many poorly established lines were run by hand compass rather than by solar compass or jake staff compass, and were paced rather than chained. Incorrectly located lines do, however, introduce error into the surveyor's plats.

In spite of its shortcomings, the original land survey represents an unusually good job, considering the equipment with which the surveyors had to work and the conditions they encountered. No one can read contemporary descriptions of these surveys, such as that of Whittlesey (Foster and Whitney 1851; 340), without feeling admiration for those who did the work. Nevertheless, the question of utility still remains to be answered.

Most cases of flagrant error probably were corrected by resurveys. Certainly where corners were found not to have been established, effort must have been made to provide the person who bought, or homesteaded, land with the boundaries of his property. However, the fact that instances must exist where surveys and notes were not corrected should impress anyone who uses them with the need to investigate the situation in the area with which he is working. In many cases, the county surveyor can provide the necessary information. At other times, it will be advisable to consult the *Annual Reports of the Commissioner and the Surveyors General of the United States General Land Office,* which are to be found in the House and Senate Documents, the Annual Reports of the Secretary of the Interior, and the separate reports of the Commissioner of the General Land Office.

Doubt has been expressed whether the trees selected as bearing trees represent a random sample —that is, whether they actually are the nearest trees to the post and were chosen without regard to species, condition, size, or other factors. The question of random has been considered by others (Sears 1925, Kenoyer 1929), but the facts will be reviewed here.

All of the original instructions plainly specify that corner posts should be, as one puts it, "of the most durable wood of the forest at hand." In the Upper Peninsula, northern white cedar was a favorite source of material; sometimes a post was obtained a considerable distance from the corner. Ironwood was a commonly used alternative, apparently on the assumption that its hardness indicated durability, but practically every other species of tree was used to some extent. The square outlines or rotted shells of these posts may sometimes be seen by carefully removing the upper portions of the soil. Occasionally an intact post point is found. It follows that there must also have been interest in the lasting qualities of bearing trees. Written record of it, however, is clearly stated only in the 1843 instructions: "You will select for bearing trees those which are the soundest and most thrifty in appearance, and of the size and kinds of trees which experience teaches will be the most permanent and lasting." The bias inherent in such an edict is clear. In 1846 and 1851, it was required only that the trees be "alive and healthy and not less than 5 inches diameter." In practice, trees of 4 inches diameter often were used, and in exceptional cases, 2 and 3 inch stems were blazed. The 1831 instructions alone state that the trees chosen in each section should be nearest the post. In 1855, as reported earlier, it is merely implied that they should be by the stipulation that measurements must be made to "two or more adjacent trees in opposite directions, as nearly as may be." Other considerations also may have influenced tree selection. In 1855, a tree supplying the place of a corner post was marked as directed for posts, unless it "should be a beech, or other *smooth* (italics in original) bark tree," in which case "the marks may be made on the bark, and the tree notched." Beech was the only species in 1850 which, on occasion, need not be blazed to provide a surface for the iron marks (identification cut into the wood with a timber scriber). Surveyors had to hew, or peel, the bark "unless the tree be beech, in which case its bark, if smooth, may remain on" and the scribing done directly on it.

In the Upper Peninsula of Michigan, one frequently finds that the bark was merely knocked off the bearing trees and the iron marks placed on the smooth, round boles. Thus, trees with "loose" bark and those with symmetrical trunks may have been selected oftener than chance would allow. In re-witnessing corners, I usually choose small trees rather than large ones when both are available and prefer small red maple or yellow birch to sugar maple or hemlock, except during the season when hemlock bark slips easily. Like many contemporaries, I use northern white cedar whenever possible and avoid the conifers which exude resin. Other surveyors and foresters have different preferences. Some select white and red pines because they are long-lived and less subject to decay; others ignore them because they are more likely to be cut. There is a general tendency to use an uncommon species where possible (*e.g.,* black cherry in the Upper Peninsula) because relocation of the corner will be easier. It is not unreasonable to believe that similar, and other, preferences were entertained among the old surveyors. Foresters and surveyors who work with land lines and who are familiar with original bearing trees are not agreed as to the impartiality with which the latter were selected. Among those with whom the matter was discussed, the majority believed there was bias, but opinions differed as to how much and in what directions.

There can be little question that the selection of bearing trees was not strictly random. It is unreasonable to assume that it should be. When two or more trees were equally handy, it is inevitable that personal preference, as well as the condition and kind of tree, should dictate to some degree the one that was picked. The question, therefore, concerns not whether bias was present, but whether it was important.

Evaluating Bias in the Surveys

By quadrant

A basic assumption, as expressed by Cottam and Curtis (1949), is that the distribution of trees in a woods deviates at random from a theoretical condition in which all trees are equidistant from all neighboring trees. A corollary is the hypothesis that the tree nearest to the corner may occur with equal frequency in any of the 4 quadrants; and it can be used to provide a simple check on the presence and magnitude of bias.

At 230 interior corners in the Hurons Block, the distribution of the nearest tree with respect to northeast, northwest, southwest, and southeast quadrants was 51, 61, 60, and 58, respectively. Analysis of chi-square indicates a difference as large as that observed (1.118) could be due to chance at least 7 out of 10 times; therefore, it is not significant. A similar check of 411 interior corners in the Misery Bay Block yielded a 108, 94, 106, and 103 tree distribution. The difference here is slightly larger (1.248)—the statistical evidence against its occurrence is about one in 4. In a third sample representing 410 corners in Muskegon County, chi-square (2.509) indicated there was only a 50 per cent probability that the 96, 97, 101, 116 distribution of trees was due to chance. Counties undoubtedly can be found where a statistically significant bias is present; therefore, recognition must be made of the risk involved when work based on the proximity of bearing trees to the corner post is undertaken.

In the above test, bias in one locality by one survey crew may be cancelled by an opposite bias in another place by a different crew. This can easily be detected by noting whether sequences of 3, 4, or 5 corners have the nearest tree in the same quadrant. There is only once chance in 64 of an event occurring 3 times in a row when there are 3 other possibilities. Similarly, the probabilities that series of 4 or 5 will happen are only one in 256 and one in 1,024, respectively. Following the sequence in which corners were set in subdivision surveys for 3 or 4 townships, a comparison with expected frequencies can be made.

Even more rapid is an inspection of the incidence of pairs of trees at corners. If the trees obviously have been reported in opposite quadrants, the probabilities that series of 3, 4, or 5 pairs will occur in northeast-southwest or northwest-southeast quadrant combinations are one in 8, one in 16, and one in 32, respectively. When the instructions did not specify that bearing trees be set in opposite quadrants, then the second tree should be found with equal likelihood in any of the other 3 quadrants. The number of possible tree combinations is 6, and the probabilities of series of 2, 3, 4, or 5 identical combinations are, therefore, one in 36, one in 216, one in 1,296, and one in 7,776, respectively. Other applications of the Theory of Probability can readily be imagined when 4 trees are reported at section corners.

By distance from the corner post

A satisfactory distribution of bearing trees with respect to quadrants, or pairs of quadrants, does not imply random selection with respect to diameter class. Whether tree size or kind accounted for bias must be determined separately. When section and quarter corners are set according to the prescribed grid pattern, smaller trees will usually occur in the vicinity more often than larger ones, but no other relationship exists between the diameters of nearby trees and their distance from the corner post. If, in a given timber type, trees of one diameter class are found at a certain mean distance from the post, then theoretically, trees of every other diameter class should be located at that same mean distance, although their frequencies will vary. Similarly, if one computes the mean distances from the post to all adjacent trees, this distance should be the same as the mean for each of the component diameter classes, so long as no preferences were exercised.

It must be emphasized that this relationship will hold for a timber type in a region, but that it will not necessarily apply to different stands within that type. It is obvious that distances from corner posts will be greater for stands in which large trees predominate than in those made up of smaller trees; and distances will usually be greater for stands on poor sites than for those on good sites because the stocking is different. Nevertheless, significant differences should not occur within the type itself because all the attainable diameters will be present and their distribution will be characteristic for that particular association of trees. This point is well demonstrated by Table III, which is based on the mean distance by diameter class of the nearest tree in each of the 4 quadrants to the centers of 78 plots randomly located in virgin northern hardwoods. There is less than one chance in 20 that the difference observed was not due to chance. The lower figures for the MX type merely reflect the prevalence of small trees on many of the plots.

Larger samples should show even greater uniformity, since a larger number of stands would be included. In climax forests even relatively small samples ought to be sufficient. It will be rare when more than a few survey corners were established in the same stand. Seemingly uniform northern hardwoods are found on close inspection really to consist of a mosaic of even-aged, or several-aged, stands a fraction of an acre or more in area rather than of an intimate mixture of single trees of different age classes. Even-aged stands of intolerant or semi-tolerant species simply occupy larger tracts and, therefore, are more conspicuous. In any case, few stands of any kind are large enough to harbor more than two or three quarter or section corners, while one corner will be the usual number. By choosing two or three hundred corners which fall within the area included in a type and by throwing out obvious misfits (*e.g.,* a corner with two larches in northern hardwoods) mean distances can be obtained and the bias, if any, can be detected.

TABLE III. Mean distance from plot center to the nearest tree of each quadrant in sugar maple (M), sugar maple-yellow birch (MB), and mixed hardwood (MX) plots located in old-growth timber

Diameter class*	TIMBER TYPE							
	M		MB		MX		Total	
	Trees	Mean† dist.	Trees	Mean dist.	Trees	Mean dist.	Trees	Mean dist.
4.......	12	19.5	5	22.6	13	18.0	30	19.4
6.......	24	25.8	10	20.1	20	18.7	54	21.4
8.......	22	20.4	5	10.4	14	17.9	41	18.3
10.......	19	19.5	5	18.6	10	16.5	34	18.9
12.......	22	26.5	8	26.0	6	16.6	36	24.9
14.......	16	21.9	9	21.1	8	24.1	33	22.2
16.......	21	22.3	2	18.0	7	17.3	30	20.8
18.......	11	17.0	7	28.9	2	24.0	20	21.8
	147	21.0	51	21.5	80	18.5	278	20.9

*There were 32 additional trees between 20 and 30 inches in diameter. The mean distance for all of them was 22.7 links

†All distances in surveyor's links (7.92 inches, or 20.12 centimeters)

If any preferences by the surveyor exist with regard to species, they can be determined in a similar way. In a timber type which contains two or more dominants, the location of each with respect to the corner post depends on the density of the trees of that species. If there were twice as many trees of one kind as of another, the frequency of the first near the post would be twice as great. However, mean distances from the post for each species and for every diameter class in it should be the same. This is wholly true only when the different kinds of trees are well distributed throughout the type. Such often is not the case for a variety of reasons. Most important are the observation that clumping—contagious distribution—is a common phenomenon and the fact that the various dominants rarely are exact ecological equivalents. In northern hardwoods, as broadly defined by foresters, it is common to find on the moister sites that some limited localities support more red maple, others more yellow birch, still others more hemlock, and so on, depending on the microhabitat and the past history of the place. Plots in small patches of hemlock show much greater variation in basal area (reaching over 350 square feet per acre, in some cases) than do patches of sugar maple (rarely as much as 250 square feet per acre), with corresponding differences in tree spacing. The mean distance from randomly located points obtained for 84 trees in hemlock stands was, for example, only 17 links compared to almost 21 links given in Table III for hardwood stands.

Segregation of microhabitats is not possible from survey data, so some error from this source may creep in undetected. Other deviation might arise from the occurrence of groups of mid-tolerant trees, like American elm, or of trees which frequently have multiple stems, as do basswood and northern red oak, all of which may be found even in a type classed as sugar maple. But minor components are usually too thinly represented in the survey notes to provide very accurate determinations anyway. Therefore, the degree of random choice cannot be computed with equal accuracy for all species. It will be most closely approximated for the ones which are the commonest, and especially for those, like sugar maple and beech, whose tolerance and habitat requirements also are similar.

The most numerous species in a type may readily be compared. Perhaps the simplest way to do this merely requires selection of one, or a few, diameter classes which from previous inspection are found to occur most frequently. Kenoyer (1929) used distances in this manner to determine if beech were preferred over sugar maple. Table IV is based on the mean distance from the post of bearing trees at interior corners in 5 Houghton County townships of the Misery Bay Block. Five diameter classes of the 3 most commonly reported species (sugar maple, yellow birch, and hemlock) are shown relative to their occurrence in two major timber types (sugar maple type and hardwood-hemlock type). Although the species exhibit wide differences in representation, the means are close. Computation of Wilcoxon Sums (Tukey 1949) indicate that differences are significant only for the 3 available yellow birch-hemlock pairs in the M type. Stand tables suggest that partiality with respect to diameter class should be shown more clearly than it is, although distances are greater for large trees than for small ones when the data for both types are pooled. This and stand tables are treated later.

A series of diameter classes, therefore, can be used to determine if a trend exists between the species in each diameter class. If none is apparent, as in Tables III and IV, then it may be assumed that any actual differences are not important. On the other hand, if bias appears to be present, its significance can be investigated statistically.

TABLE IV. Mean distance (links) of bearing trees from the corner post for the commonest species and diameter classes in the two major types of the Misery Bay block

Diameter class	SUGAR MAPLE		YELLOW BIRCH		HEMLOCK		TOTAL	
	Trees	Mean dist.	Trees	Mean dist.	Trees	Mean dist.	Trees	Mean dist.
	Sugar maple (M) type							
6.......	4	18.8	2	16.5	..	....	6	18.0
8.......	31	25.6	3	25.3	..	....	34	25.5
10.......	62	24.5	6	32.3	6	20.6	74	24.7
12.......	65	26.6	8	25.5	1	25.0	74	26.5
14.......	36	22.9	8	27.7	1	25.0	45	23.9
	198	24.9	27	27.0	8	21.7	233	25.1
	Hardwood-hemlock (MH) type							
6..	2	16.0	1	14.0	3	23.0	6	19.1
8.......	19	16.6	6	14.2	10	23.3	35	18.1
10.......	47	21.3	16	25.6	10	24.2	73	22.6
12......:	57	24.5	18	21.1	28	26.3	103	24.3
14.......	37	27.6	9	20.5	28	26.3	74	26.2
	162	23.2	50	21.4	79	25.5	291	23.5

There are two other factors which introduce error into analysis of survey notes by diameter class, and to a somewhat lesser extent, by species. Both are concerned with the manner in which the measurements are obtained. As mentioned earlier, bearing tree distances were actually taken to a notch cut in the tree rather than to its center. Larger trees, therefore, would appear to be closer than smaller ones unless a correction for the radius is made. The difference is not important when only linear measurements are involved and is inconsequential when analysis is restricted to a sequence of 3 to 5 of the most commonly occurring diameters. If the measurements, or figures derived from them, are to be squared, as in calculation of basal area, the correction must be made, because the percentage error can be serious when short distances and large trees are involved. The error will be eliminated if a single diameter could furnish the required information.

More serious is the degree to which diameters recorded in the survey notes approximate those actually represented in the bearing trees, since only estimates were required by the survey instructions. It has been demonstrated that good estimates cannot consistently be made, particularly on large trees, unless repeated checking is done. There is no evidence that surveyors ever made such checks, although they carried a tape for measuring short distances (Burt 1855). It even seems likely that, in spite of the tape, distances greater than 30 links often were estimated also. An analysis of the distances from the post for 571 10, 12, and 14 inch bearing trees showed excessive frequencies for 35, 40, 50, and 60 links, although frequencies at shorter distances were close to expectation. When trees were not near at hand, the distances to them may have been paced or guessed. It is common experience that errors of estimate tend to be compensating. Although early survey crews probably did little or no checking, compensating error undoubtedly characterized their estimates. There is no way of proving, however, whether the points of compensation were coincident with the diameters they represented, but stand tables provide one basis for judgments.

By stand tables

When stand tables are drawn from survey data, they can be compared with existing tables representing virgin timber, or with some based on as many remnant stands as can be found. The danger in assuming that one, or a few, small stands will give an accurate picture of the timber type is obvious. Data as good as that in Table II are not ordinarily available, but less detailed information often can be obtained and usually is usable. Table V shows the distribution of trees by species for all townships of the Misery Bay Block. Only interior corners which fell in the hardwood-hemlock and the sugar maple types were used, since this would provide data roughly equivalent to the northern hardwoods of Table II. Odd-numbered diameters were apportioned equally between the next higher and next lower classes. Even casual inspection reveals that conspicuous modes appear at 20, 24, 30, and 36 inches, while the 4, 6, and 8 inch classes definitely are under-represented. The frequent recording of trees in certain large, even-numbered diameter classes is a common feature of survey data. In most instances, it attests primarily to the inability of men to estimate large diameters accurately, but the irregularities can be smoothed. In disturbance types (*e.g.,* jack pine or aspen), however, the curve may represent a composite of the diameter ranges for several widely spaced age groups which originated as a result of fire, or from other causes. Irregularities will be most marked when the number of stands are few and the size of each is great. When large areas containing many stands are considered, so many age groups will be encountered that a curve representing all of them would tend to smooth out anyway. When a smoothed curve for the data in Table V is compared with one based on Table II, the curve segments for the large diameter classes are similar. There is a striking over-representation in the 12 inch class, however, and to a lesser extent, in the 10 and 14 inch classes. Increasing under-representation characterizes the 8, 6, and 4 inch trees.

TABLE V. Stand tables for bearing trees in the sugar maple (M) and hardwood-hemlock (MH) types, Misery Bay Block

Diam. class	SUGAR MAPLE		YELLOW BIRCH		HEMLOCK		ALL OTHERS*		TOTALS	
	M	MH	M	MH	M	MH	M	MH	M	MH
4......	0.5	1.0	...	...	1.0	1.5	...	...	1.5	2.5
6......	4.5	2.0	2.0	1.0	...	4.5	1.0	4.0	6.5	10.5
8......	25.0	26.0	2.5	7.0	...	7.0	11.0	25.5	29.0	45.0
10......	68.5	61.0	6.5	19.0	5.0	22.0	15.0	66.0	83.5	112.5
12......	61.5	68.5	7.0	26.0	1.0	34.5	9.0	35.0	76.5	145.0
14......	40.5	50.0	6.0	9.5	1.0	31.5	3.0	22.5	50.5	102.5
16......	13.0	32.5	3.0	8.5	1.0	18.0	2.0	11.0	19.0	66.0
18......	6.5	7.0	4.0	...	1.0	14.0	1.0	4.0	12.5	24.0
20.....	8.0	10.0	...	8.0	1.5	27.0	4.0	2.5	12.0	50.0
22......	...	1.0	...	...	0.5	2.5	0.5	1.0	1.0	4.5
24......	1.0	5.5	...	3.0	...	5.0	...	1.0	1.0	14.5
26......	...	0.5	...	...	...	1.5	...	...	...	2.0
28......	...	...	...	...	...	1.0	...	...	...	1.0
30......	1.0	1.0	3.0	2.0	1.0	8.0	1.0	...	6.0	11.0
32......	...	...	...	1.0	...	1.0	...	...	...	2.0
34......	...	...	...	...	...	...	...	...	...	...
36......	...	1.0	...	...	...	3.0	...	1.0	...	5.0
40+....	...	...	...	...	...	1.0	...	1.0	...	2.0
Total.	230.0	267.0	34.0	85.0	13.0	183.0	46.0	181.0	299.0	600.0

*Chiefly balsam fir, northern white cedar, white spruce, and elm

All of the surveyor's instructions required that information similar to the following be placed on each bearing tree:

R36W
T54N
S36

This, of course, is a condensation of Range 36 West, Tier 54 North, Section 36. Sometimes the tier number was placed first. It is very difficult, nevertheless, to put that many characters on the round bole of a 4 or 6 inch tree, since a timber scriber makes figures about an inch and a half wide. Even on an 8 inch tree there is hardly enough room, unless a large blaze is made, which may imperil the life of the tree (to save space, however, letters often were inscribed on the diagonal). At quarter corners, on the other hand, discrimination against small trees should be less pronounced because the only identification required was "¼ S." One should also expect small stems to be used less frequently at interior corners where trees in all 4 quadrants were available than at corners on township and range lines where it was customary to locate both bearing trees in the township being laid out. On a range line, for example, bearing trees were chosen in adjacent quadrants on the west side of the line.

The occurrence of small diameter trees at all corners in the Misery Bay Block, except those in conifer swamps, is shown in Figure 3. The data bear out all of the above assumptions. This suggests that in northern hardwoods, and in other

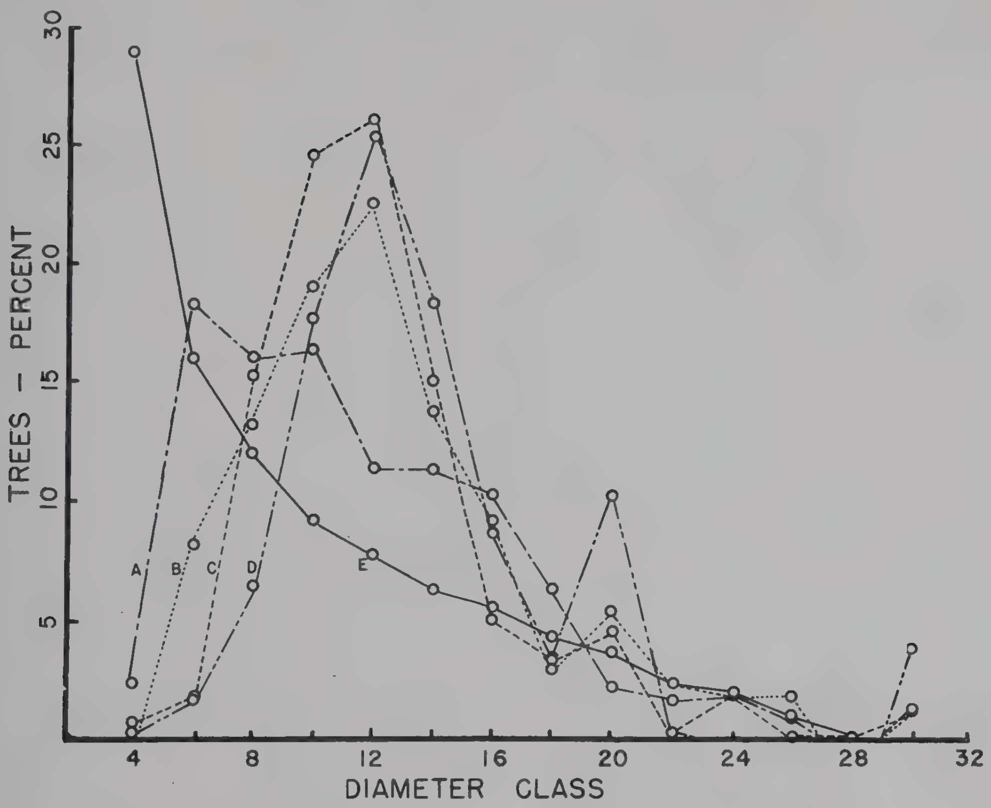

FIG. 3. Relation of size of bearing tree to kind of corner, Misery Bay Block. Lines A and B connect points representing quarter corners and section corners, respectively, of the township and range line survey. Lines C and D join quarter corners and section corners, respectively of the subdivision survey. The points joined by line E represent old-growth northern hardwoods data from Table II.

timber types where a similar density of stems and range of diameters is to be expected, the trees reported at quarter corners will give a better approximation of the distribution of diameter classes, while the best one would be obtained by using only quarter corners on exterior lines. Among large stems, the distributions at all 4 groups of corners are similar, and they follow the expected trend rather well. If the distributions were smoothed to compensate for the excessive reporting of certain diameters, the similarity between the curves for bearing trees and the one for the "standard" would be even more apparent.

Other comparisons are given in Table VI, where bearing trees in the Alberta and Huron Blocks are analyzed by species, diameter class, and location at corners. In both blocks, 6 and 8 inch trees of each species show a marked tendency to occur closer to the post than do larger stems. Mean distances for small trees at quarter corners are not consistently less than at section corners, but the relative numbers of trees is greater (at quarter corners). This supports conclusions drawn earlier.

Of further interest are the mean distances for all trees in each block. The average for the Alberta Block is 22.8 links, which is close to the 24.2 links obtained for Misery Bay timber. However, the 32.5 links in the Hurons Block suggests much more open timber, or at least, smaller and noncontiguous stands. Actually, the latter interpretation is correct, as has already been mentioned. Furthermore, it is the more reasonable interpretation whenever, in comparing two nearby areas, large differences are found in the spacing of timber which other factors indicate should be similar. Corners were not set with reference to type lines. Where the land is rugged or broken, a surprising number of them are found in situations which are not indicative of the surrounding timber. Often no clue to these differences can be found in the field notes. A corner may, for example, fall in a small natural opening, near the summit of a small rocky knob, or in a brushy seepage near a spring, but

TABLE VI. Bearing tree distance from the post at quarter corners and section corners in the Hurons and Alberta blocks with respect to species and diameter

Diam. class*	QUARTER CORNERS						SECTION CORNERS						TOTAL	
	Sugar maple		Yellow birch		Hemlock		Sugar maple		Yellow birch		Hemlock			
	Number	Mean dist.	Number	Mean dist.	Number	Mean dist.	Number	Mean dist.	Number	Mean dist.	Number	Mean dist.	Number	Mean dist.
	Hurons Block													
6.......	14	21.6	3	31.0	2	10.0	6	35.8	3	33.3	..	....	28	26.1
8.......	26	25.4	7	28.1	3	12.7	12	23.7	..	....	..	....	48	24.6
10.......	22	48.5	4	43.2	1	17.0	22	35.8	5	28.8	1	34.0	55	40.5
12.......	22	36.2	6	37.0	3	13.7	13	27.4	1	81.0	..	....	45	33.3
14.......	12	29.3	2	75.0	..	....	9	38.0	6	30.3	..	....	29	35.3
	Alberta Block													
6.......	10	18.1	5	18.0	7	19.4	2	15.5	1	9.0	3	19.0	28	18.0
8.......	10	18.7	6	14.2	3	22.7	3	24.3	1	21.0	2	17.5	25	18.8
10.......	10	28.1	9	25.3	8	21.5	7	34.7	2	16.0	8	29.8	44	27.1
12.......	12	25.9	11	13.3	8	19.9	10	34.9	12	30.0	7	22.3	60	24.7
14.......	8	21.4	6	19.5	4	17.2	1	17.0	2	22.5	5	19.0	26	19.8

*In the Hurons Block there were 67 trees larger than 14 inches; the mean distance for the 273 trees 6 inches or larger was 32.1 links. There were 81 trees larger than 14 inches in the Alberta Block; the mean distance for the 264 trees 6 inches or larger was 23.4 links

the bearing trees may be located in a sugar maple stand surrounding the area because no trees were available near the post. In such cases one would justifiably map the corner within the sugar maple type, but the *distance* to a bearing tree would be excessive. Obviously, mean distance will appear to be greater than it should be.

In view of tree diameter-corner relationships shown in Figure 3, it follows that whenever discrimination against trees of small diameter can be shown, then discrimination must inevitably occur, especially in mixed stands, against those species which characteristically never attain large size. Logical though this reasoning may be, none of the study blocks provided a conclusive demonstration of it. It will be remembered that on line trees only two blazes were required, one directly above the other, and no scribing was done. Diameter, therefore, should be even less important in the selection of line trees than of those at quarter corners. If balsam fir always were chosen at random by the surveyors, then the ratio of fir bearing trees to line trees should be 6 to 8—the ratio in an average section when only two bearing trees were reported at each corner and two line trees on each half mile of line. However, in the Keweenaw Point and Hurons blocks where spruce-fir stands are common, there were at least as many fir bearing trees as line trees, which is decidedly contrary to expectation. Similarly, in the Misery Bay Block where fir grows chiefly as an understory tree, the species was reported 62 times as a bearing tree and only 55 times as a line tree. On the other hand, fir appears as a bearing tree at quarter corners in the Misery Bay Block 4 times as often as it does at section corners, while a ratio of two to one would be expected. When conflicting results are obtained, a safe conclusion cannot be drawn; but the tests are easy to apply and ought to be useful, especially when investigating species associations by random pairs (Shanks 1953).

Diameter differences are of little or no importance in even-aged stands, because the diameters of most of the trees will be very close to the mean for all. Over 75 per cent of the trees in jack pine stands deviate no more than 2 inches from the mean diameter, even when the latter is as great as 10 inches (Eyre and LeBarron 1944). When the mean is smaller, the percentage increases. Species preferences obviously cannot be satisfied in pure jack pine stands either. Good comparisons, therefore, should be obtainable between present and former stands, even though no "virgin" timber is available for comparison today.

Table VII presents the diameter class distribution and mean distance from the post for jack pine bearing trees at interior corners on sand plains in the area. Not included in the table are 9 trees which were located 150 links or more from the post—presumably across small openings. Mean distances by diameter class are close—in fact, chi-square reveals that a larger deviation due to chance has a 99 per cent probability. Therefore, it is reasonable to assume that Table VII represents a good approximation of the stands which existed a hundred years ago. No one inch trees (half of which would have been included)

TABLE VII. Distribution of jack pine bearing trees by diameter class at quarter corners and sections corners on Sand Plains and their mean distance from the corner post

Diameter class*	QUARTER CORNERS		SECTION CORNERS		ALL CORNERS	
	Number	Mean dist.†	Number	Mean dist.	Number	Mean dist.
2........	5.5	45.6	2.5	40.4	8.0	44.0
4........	15.0	49.7	8.0	45.0	23.0	48.0
6........	15.0	34.2	9.0	63.4	24.0	45.2
8........	31.0	43.0	6.5	32.3	37.5	41.2
10........	15.5	47.2	13.0	45.5	28.5	46.7
12........	13.0	41.2	2.0	75.0	15.0	45.6
14........	2.0	45.5	...	....	2.0	45.5
16........	...	....	...	....	...	....
18........	1.0	61.0	...	....	1.0	61.0
	98.0	43.4	41.0	48.1	139.0	44.8

*Uneven diameters were divided between the adjacent even-numbered classes
†Links

were reported, so values for the 2 inch class probably are low. A Wilcoxon Sum indicates that no significant differences occur between the pairs of trees at quarter and section corners. Only 9 plots at corners in present stands were available for comparison. They suggest that mean diameter today is not as great (less than 7 inches against more than 8 inches) and that stands are denser (mean distance of 31 links against 45 links in Table VII).

SUMMARY AND CONCLUSIONS

Two facts are clear concerning the General Land Office Survey:

1. The procedure of the survey was not everywhere the same—until 1855, surveying procedure was not fully standardized and instructions to survey crews were changed from time to time. 2. Surveyor's trees were not truly random selections when the instructions relating to their establishment were followed—where random apparently is present, it is due to accident rather than to the conscious avoidance of bias. In some instances, unreliable surveys resulted from slip-shod work or fraud. Obviously, these are not usable.

Each worker who refers to survey records must, therefore, acquaint himself with the procedure of the survey in the area he studies; and he must establish the validity of the data he uses. The primary question will concern not whether bias is present, but whether it is important. Conclusions reached in one area cannot safely be cited in another as evidence that the surveys for both are equally useful.

The random in the placement of bearing trees with respect to quadrant can be analyzed for a series of corners by application of probability theory. More or less bias will be found, but it will not usually be very strong. Surveyor's preferences with regard to species and tree size can readily be determined by computing mean distance from corner posts to their respective bearing trees. In many, if not most, timber types species preferences will not prove to be important because the choice of species adjacent to a corner was limited. Surveyors were decidedly partial to medium-sized trees, however, when a range of diameters was available. Small trees of any species were avoided because the required corner identification was too difficult to inscribe on them; very large trees often were rejected because they provided a poor surface for inscription or because they were poor risks. Species which seldom attain large size were likely to be discriminated against unless they grew in pure groups or stands.

Tree diameters were estimated by the surveyors. Stand tables indicate that certain diameters were estimated with excessive frequency, but in many cases this error can be adjusted by smoothing the distribution curve. Sometimes the chainage from corner post to the more distant bearing trees also was guessed or paced. In the areas studied, this was evident chiefly for trees farther than 30 links (19.8 feet) from the corner post. The assumption that bearing trees are random pairs is not justified when diameter class (or species) preferences are marked or when the bearing trees consistently are reported in opposite quadrants and only two per corner were established.

Although true random is not an attribute of the General Land Office Survey, the survey records do constitute a sample of the vegetation recorded on the spot according to a predetermined plan. Valid quantitative analyses of the vegetation the surveyors saw are possible when the bias inherent in the methods they used is small or has no effect on the inferences drawn; or if the bias itself can be used to advantage. If a worker fails to investigate the kind and degree of bias beforehand, however, his conclusions are liable to contain errors that could easily have been avoided.

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EFFECTS OF BURNING ON A DESERT GRASS-SHRUB RANGE IN SOUTHERN ARIZONA

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Introduction

Encroachment of undesirable woody plants into former grasslands is a serious problem on western rangelands. These woody plants dominate the site and reduce perennial grass cover. The result is a loss in grazing capacity and livestock production.

The problem of invasion and increase of mesquite (*Prosopis* spp.),[3] cactus (*Opuntia* spp.), and burro-weed (*Aplopappus tenuisectus*) on certain rangelands of southeastern Arizona has been recognized for many years (Fig. 1). In spite of considerable experimental work, there is still need for better chemical, mechanical, or biological methods for eradication or control of these woody invaders. Fire as a tool for control has been investigated to some extent. Additional information is needed as to how, when, and where fire should be employed. This paper reports the effects of fire upon several undesirable woody plants, palatable range vegetation, and soil for an area of the Santa Rita Experimental Range, 35 miles southeast of Tucson, Arizona.

The Problem

Repeated fires on slopes of the low foothills of this region may have been responsible for holding back the invasion of shrubs and trees and maintaining a grass cover. Shortly after the establishment of the Santa Rita Experimental Range in 1905, Griffiths (1910) observed that shrubs, particularly mesquite, were increasing, presumably as a result of fire prevention. A few years later, Wooton (1916) observed that Griffiths' prediction of a woody plant invasion was coming true.

The extent and seriousness of the invasion of southern Arizona rangelands by mesquite, cane cholla (*Opuntia spinosior*) and jumping cholla (*O. fulgida*), pricklypear (*O. engelmannii*), and burro-weed have been determined (Upson, Cribbs, and Stanley 1937). In a systematic survey of 12,034,000 acres, occupancy by various shrubs was estimated to be as follows: burro-weed, 5,494,000 acres; cactus, 1,116,000 acres; and mesquite, 9,187,000 acres. Also, interviews indicated that the majority of local stockmen were aware of a considerable increase and spread of shrubs during the past 50 years.

More recent measurements show the rate of increase of undesirable plants on selected study sites of the Santa Rita Experimental Range. According to Glendening (1952), increases of woody plants for cattle exclosures during the 20 years preceding 1949 were:

Species	*Percentage increase*
Mesquite	124
Jumping cholla	72
Cane cholla	236
Pricklypear	47

Recent observations on the Sata Rita Experimental Range show that perennial grass production, resulting from the presence of woody plants, may be lowered as much as 25 per cent by burro-weed, 10 per cent by cactus, and 100 per cent by mesquite. Even with the forage replacement by foliage and fruits of mesquite, a loss of two-thirds of potential grazing capacity may result. Woody plants are also a poorer soil-protective cover than the grasses. Shrub encroachment thus leads to more flash runoffs and increased erosion.

Previous Work

Thornber (1907), working in southern Arizona, observed that fire seemed effective for killing burro-weed and mesquite. Wildfires were believed to have been common on mesas and foothills in the past because of abundant remains of charred stumps (Thornber 1910). Wooton (1916), working on the Santa Rita Experimental Range, noted that occasional fires were severe enough to top-kill mesquites 10 to 12 feet tall and usually killed smaller bushes back to the ground.

Parker (1939) obtained 100 per cent kills of burro-weed by burning plants drenched with stove oil in May. By applying a kerosene torch to the

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[1] These studies were originated by G. E. Glendening and some of the data were collected by Mack E. Roach, formerly Range Conservationists, of the Rocky Mountain Forest and Range Experiment Station. Computations were by Mrs. Geraldine Peterson, Statistician for the Station. The assistance of R. R. Humphrey of the University of Arizona who critically reviewed the manuscript is also gratefully acknowledged.

[2] Forest Service, U. S. Department of Agriculture, with headquarters at Colorado A. & M. College, Fort Collins, Colorado. Research reported here was conducted in cooperation with the University of Arizona and three independent stockmen.

[3] Nomenclature follows Kearney and Peebles (1951). The mesquite on the study was velvet mesquite (*P. juliflora* var. *velutina*).

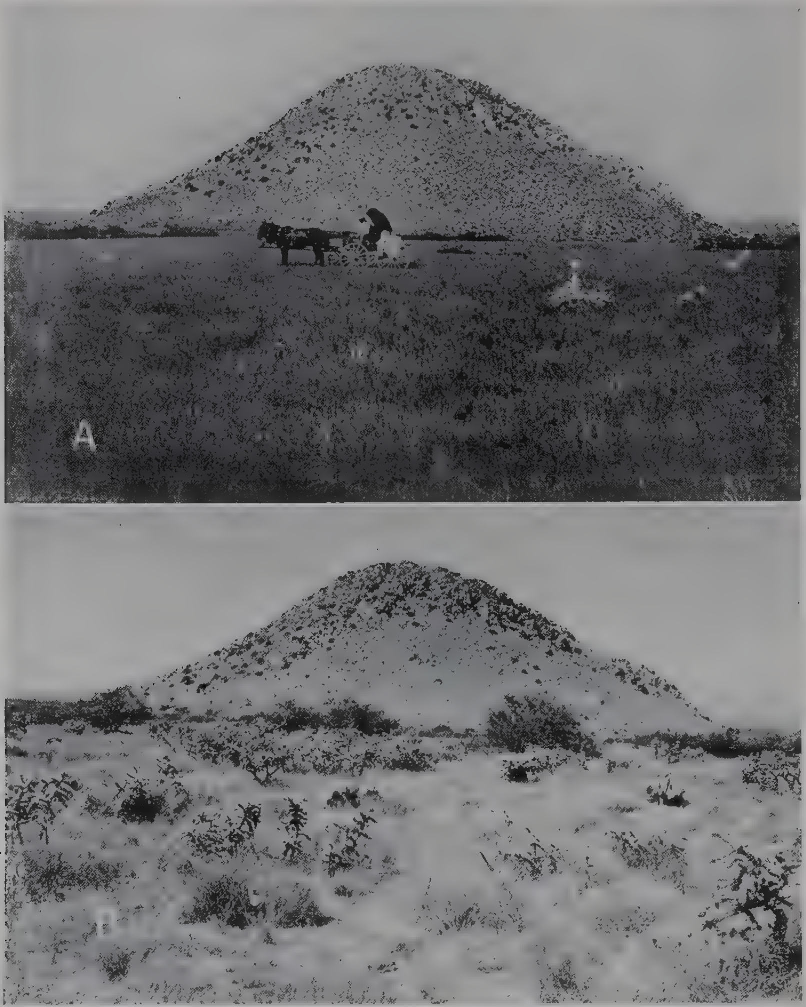

Fig. 1. Increases in woody plants during a 38-year period on a site immediately adjacent to the study area. (A) In 1903, mesquite (m) was confined to washes, cactus (c) was rare, and burro-weed absent. (B) By 1941, mesquite was moving up on the mesas, cane cholla (c) and pricklypear (p) had increased greatly, and burro-weed (b) had invaded the site.

base of mesquite trunks, Streets and Stanley (1938) obtained 40 per cent kills but their results were extremely erratic. Ignition of trees sprayed with kerosene or diesel oil by these workers gave very low plant kills.

Humphrey (1949) reported that general notes of a 1933 burn on the Beach Ranch southeast of Tucson, Arizona, indicated that a fire there had killed all burro-weeds and approximately 50 per cent of the cholla and mesquites. In 1935, total number of perennial grass plants was considerably higher on the burned as compared to the unburned area. On another small burn, in the Sierrita Mountains southwest of Tucson, burro-weeds were reduced in the ratio of 71 to 1 and an estimated 75 per cent of cholla and mesquites were killed. Among perennial grass species, black grama (*Bouteloua eriopoda*), bush muhly (*Muhlenbergia porteri*), Arizona cotton grass (*Trichachne californica*), and tangle-head (*Heteropogon contortus*) decreased as a result of burning; whereas Rothrock grama (*B. rothrockii*) and three-awn grasses (*Aristida* spp.) increased.

Humphrey and Everson (1951) burned a small planting of Lehmann love grass (*Eragrostis lehmanniana*) near Oracle. They found that fire decreased burro-weed 73 per cent, jumping cholla 29 per cent, cane cholla 7 per cent, and pricklypear cactus 9 per cent. The stand of Lehmann love grass was reduced by about one-third on the burned area, but it increased by one-fourth on an adjacent check area. Glendening and Paulsen (1955) fired 750 pounds of straw per acre bunched around the crowns of individual mesquites during the months of February, June, and November. Mesquites were found to be most susceptible to fire in June. The mesquite of different size classes killed by this method of burning during June was as follows:

Basal stem diameter in inches	*Percentage killed*
0 to 0.5	52
0.5 to 2	15
2 to 4	8
4 to 6	11
More than 6	14

Experimental Areas

Experimental burns were made at two sites designated "Area A" and "Area B." Area A was located at an elevation of about 3,700 feet on the Santa Rita Experimental Range. Slightly over 100 acres was broadcast burned between two shallow arroyos bordering a gently sloping mesa, and an adjacent area was left unburned as a check. Soils are Tumacacori and Whitehouse coarse sandy loams. The Tumacacori series is slightly superior for plant growth but both soils absorb, hold, and release moisture well, and are sufficiently rich in humus and nitrogen to support a vigorous plant growth (Youngs, *et al.* 1936). Area B was an enclosure of 6 acres on the experimental range which had been protected from grazing since 1929. The area is located at an elevation of 3,600 feet.

Rothrock grama, black grama, Arizona cotton grass, and a number of species of perennial three-awns were the predominant perennial grasses on Area A at the time of burning. Perennial grasses of Area B prior to burning consisted primarily of black grama, Arizona cotton grass, and various perennial three-awns.

Abundance of undesirable woody species on the two areas at the time of burning was as follows:

Species	*Plants per acre*		*Crown canopy cover, in per cent*	
	Area A	Area B	Area A	Area B
Burro-weed	3,200	900	8.0	2.3
Cholla	400	20	0.5	0.1
Mesquite	70	50	3.5	2.2
Pricklypear	110	30	0.4	0.1

Both areas generally have high temperatures, long frost-free periods, low humidity, and scarce rainfall. Average mean monthly temperatures for July are about 80° F. and January temperatures are less than 40° F. which results in a frost-free period from March to November. Evaporation from a free water surface is often in excess of 85 inches per year. During the past 30 years annual rainfall has varied from 7 to 27 inches. Nearly 60 per cent of this rain falls during June through September.

Growing season rainfall (June-September) has the greatest effect on vegetation. The tabulation below gives growing season rainfall in inches for the study years as well as the 30-year average:

	Inches of seasonal rainfall	
Year	*Area A*	*Area B*
1950	–	9.09
1951	–	7.07
1952	5.48	5.60
1953	5.55	4.86
1954	9.49	9.52
1925-1954 Average	7.05	8.14

Rainfall conditions for the years of 1951-1953 were below average. The year 1954 was the first since 1950 that rainfall was above average.

Methods and Procedures

Area A was burned at midday on June 30, 1952. At the time of burning, gentle winds less than 8 miles an hour were blowing up the slope, and relative humidity was approximately 15 per cent. Available fuel, measured in terms of annual grasses, perennial grasses, and burro-weed, approximated 600 pounds per acre (Fig. 2). Fires were set by kerosene torch progressively downslope along lines about 100 yards apart resulting in a broadcast burn.

Vegetation on Area A was measured before and after burning on randomly located, permanent transects, distributed equally between burned and adjacent unburned areas. Perennial grasses and shrubs were measured by the line transect method (Canfield 1950). Mesquite, cactus, burro-weed, and other shrubs were counted on belt transects. Herbage production of perennial grasses and other palatable species was measured on sample plots along the transects. The area was lightly to moderately grazed by cattle in the fall and winter months throughout the period of study.

Four acres of Area B were burned in June, 1950, and 2 acres were retained unburned as a check. Because the area was small, much of the firing had to be done by hand to obtain a complete

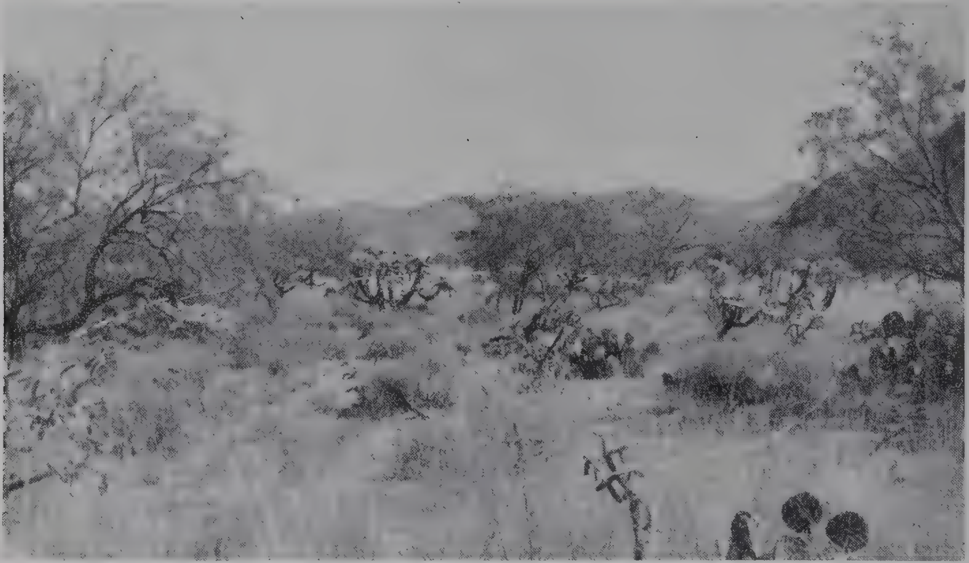

FIG. 2. Large mesquites compete with perennial grasses within a perimeter of 15 to 30 feet. When several mesquite trees grew adjacent to each other, there was insufficient fuel to carry a fire and unburned "islands" (within "dashed" line) resulted.

burn. Accordingly, the burn is believed to be more representative of the effects of fire on herbaceous plants than on woody vegetation. Measurement techniques were similar to those used for Area A. In the remaining discussion, results are for Area A unless Area B is specifically mentioned.

EFFECT ON NOXIOUS PLANTS

Fire kill of various species of undesirable woody plants on Area A 2 growing seasons after burning is tabulated below:

Species	*Percentage killed*
Burro-weed	88
Barrel cactus	67
Jumping cholla	44
Cane cholla	42
Pricklypear cactus	28
Velvet mesquite	9

Burro-weed, with 88 per cent kill, suffered the greatest loss from burning. Barrel cactus (*Ferocactus wislizeni*) loss of 67 per cent is partially the result of removal of spines by the fire. This permitted grazing animals to feed on the palatable pulpy interior of the plants and greatly increased kill. Chollas, with 42 and 44 per cent kill, were intermediate in susceptibility to fire. The comparatively low kill of pricklypear (28 per cent) was partly the result of the high moisture content of the pads, plus their habit of rooting when they come in contact with the soil. Variation in the effect of fire upon mesquite trees of different basal stem diameters is shown in Figure 3. Plant kill was confined to trees of less than 6 inches in diameter at the base, and there was little difference in kill among size classes below this limit. All

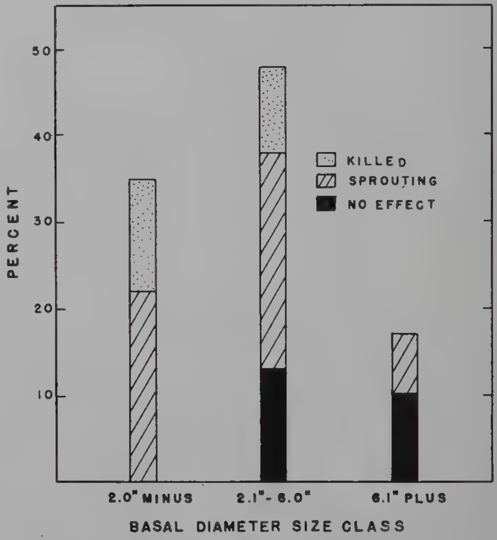

FIG. 3. Effect of broadcast burning upon mesquites of different basal stem diameters expressed as per cent of total number of plants.

trees below 2 inches were affected by burning although about 60 per cent of them sprouted. Pecentages of trees within a size class showing no fire damage increased in the larger size classes.

Effect on Forage

Vigor and density of perennial grasses were reduced the first fall (1952) as a result of burning and below-average summer rainfall (Fig. 4). In spite of unimproved rainfall conditions by the fall of 1953, there was some recovery in density and vigor of perennial grass vegetation. Summer rainfall during 1954 was about 135 per cent of average and the response of perennial and annual grasses was excellent.

Density

The composite of all perennial grasses on Area A showed a marked reduction of basal density by the first fall after burning. Total perennial grasses on the check area did not show a similar reduction. One year later, density on the burn had improved even though the density on the check area was considerably less because of weather conditions. At the end of the third growing season, density on the burned area and the check area was again about the same.

The densities of individual species of perennial grasses were not affected the same by burning (Table I). Rothrock grama and Arizona cotton grass densities were reduced the most, while the density of Santa Rita three-awn (*Aristida glabrata*) actually increased. In 1954, plant composition was still changing. Most species had increased in density in 1953 and then decreased because of weather. However, Santa Rita three-awn, other three-awns, and Arizona cotton grass were increasing in abundance relative to their densities on the check area.

Prior to burning, the perennial grass composition of Area B was much different from Area A with black grama and Arizona cotton grass dominating. Total density of perennial grasses of Area B was reduced markedly by burning (Table II). Prior to the burn, it was 138 per cent of the check, while by the end of the first (1950) growing season it was only 38 per cent of it. Arizona cotton grass and other perennial grasses, except black grama, regained original densities by the end of the 1953 growing season. In 1954, black grama still had a seriously reduced density. As a result the original total density of perennial grasses was not completely restored.

False-mesquite (*Calliandra eriophylla*) was the only palatable shrub abundant enough for significant sampling on Area A. Crown intercept of this species was reduced considerably by burn-

Table I. Effect of burning upon density of perennial grasses and a palatable shrub on Area A

Species and treatment	BEFORE BURN	AFTER BURN		
	June 1952 (Per cent)	October 1952 (Per cent)	October 1953 (Per cent)	October 1954 (Per cent)
Santa Rita three-awn				
Check (density*)	0.53	0.53	0.42	0.08
Burn (density*)	0.35	0.47	0.53	0.24
Per cent of check	66.0	88.7	126.2	300.0
Other three-awns				
Check (density*)	0.28	0.26	0.31	0.07
Burn (density*)	0.52	0.14	0.15	0.09
Per cent of check	185.7	53.8	48.4	128.6
Rothrock grama				
Check (density*)	0.57	0.68	0.55	0.48
Burn (density*)	0.39	0.30	0.41	0.31
Per cent of check	68.4	44.1	74.5	64.6
Arizona cotton grass				
Check (density*)	0.33	0.32	0.27	0.12
Burn (density*)	0.24	0.14	0.14	0.11
Per cent of check	72.7	43.8	51.8	91.7
Other perennial grasses				
Check (density*)	0.08	0.04	0.07	0.05
Burn (density*)	0.27	0.09	0.13	0.07
Per cent of check	296.3	225.0	185.7	140.0
All perennial grasses				
Check (density*)	1.80	1.83	1.62	0.80
Burn (density*)	1.76	1.13	1.37	0.81
Per cent of check	97.8	61.7	84.6	101.2
False-mesquite				
Check (density*)	0.59	0.92	0.73	0.71
Burn (density*)	0.36	0.07	0.41	0.75
Per cent of check	61.0	7.6	56.2	105.6

*Basal intercept on line transects (Canfield 1950)

Table II. Effect of burning upon density of perennial grasses on Area B

Species and treatment	BEFORE BURN	AFTER BURN			
	June 1950 (Per cent)	October 1950 (Per cent)	October 1951 (Per cent)	October 1953 (Per cent)	October 1954 (Per cent)
Black grama					
Check (density*)	0.81	0.60	0.80	0.74	0.62
Burn (density*)	1.36	0.23	0.40	0.46	0.23
Per cent of check	167.9	38.3	50.0	62.2	37.1
Arizona cotton grass					
Check (density*)	0.41	0.27	0.20	0.20	0.13
Burn (density*)	0.47	0.15	0.26	0.53	0.34
Per cent of check	114.6	55.6	130.0	265.0	261.5
Other perennial grasses					
Check (density*)	0.14	0.17	0.10	0.05	0.03
Burn (density*)	0.04	0.02	0.04	0.05	**
Per cent of check	28.6	11.8	40.0	100.0	6.7
Total perennial grasses					
Check (density*)	1.36	1.04	1.09	0.99	0.78
Burn (density*)	1.88	0.40	0.73	1.05	0.57
Per cent of check	138.2	38.5	67.0	106.1	73.1

*Basal intercept on line transects (Canfield 1950)
**Less than 0.005 per cent

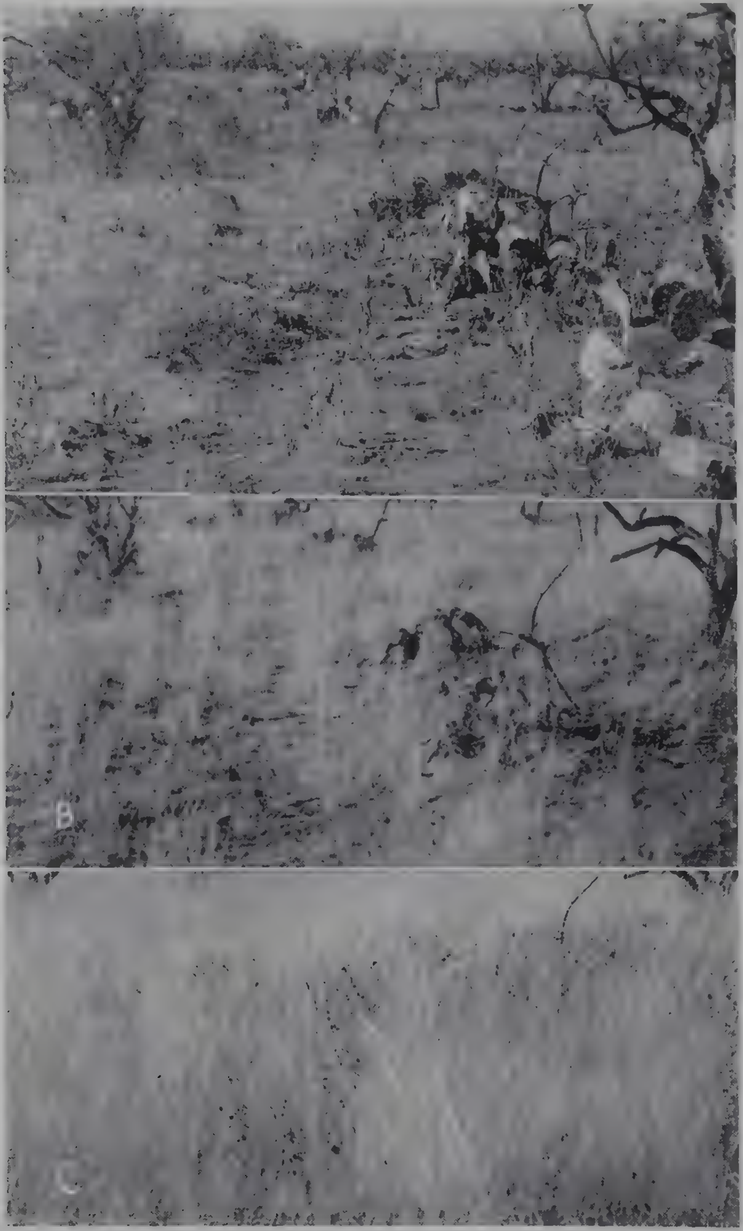

Fig. 4. Vegetational changes on burned area. (A) Fall, 1952. Density and vigor of herbaceous vegetation were reduced as a result of burning and below-average rainfall. (B) Fall, 1953. Although rainfall was below average in 1953, herbaceous vegetation made considerable gains in vigor and density. (C) Fall, 1954. With rainfall conditions about 135 per cent of average there was a striking response of herbaceous vegetation.

ing (Table I). Loss in crown density was virtually regained 1 year later. By the fall of 1954, the crown intercept of false-mesquite on the burned area was greater than that on the check area.

On desert-grass rangelands, black grama, Arizona cotton grass, and Santa Rita three-awn are desired species because of their greater stability and palatability. The other three-awns and Rothrock grama fluctuate greatly with weather conditions, and are not taken so well by cattle. Where there was a high proportion of Arizona cotton grass, the fire did not have a lasting effect on the desired perennial grasses because that species recovers quickly from burning. However, where black grama constituted a large proportion of the comopsition, the fire seriously damaged the range. Black grama was seriously affected by the burn and recovered slowly.

Herbage production

The first year after burning, herbage production of perennial grasses on the burned area was about 80 pounds per acre, which was about half the production on the check area (Fig. 5). One year later in 1953, as a result of density and vigor increases, perennial grass production on the burned plot was equal to that on unburned areas.

In the third year after burning, perennial grass production on the burned area had not yet exceeded the unburned check area. However, about 140 pounds more of annual grasses was produced on the burned than on the unburned area in 1954. Eventually, growing space occupied by annual grasses may be taken over, at least in part, by perennial grasses.

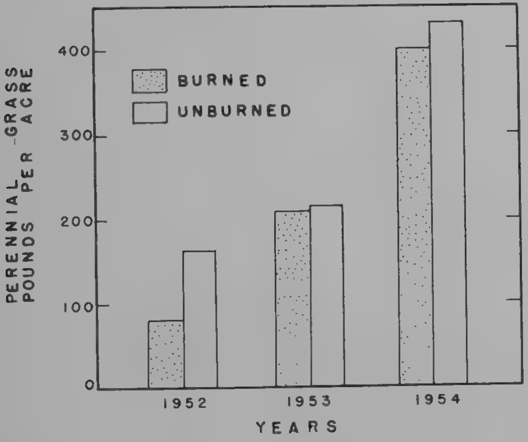

FIG. 5. Comparison of perennial grass production on Area A for three growing seasons after burning.

In 1954, forage production of palatable shrubs was only slightly greater on the check areas, although the difference was statistically signficant. Palatable shrubs on the burned area evidently had not entirely recovered their previous vigor.

EFFECT ON SOIL

Total soluble salts, organic carbon, nitrogen, potash, and pH were measured before and after burning on Area B (Table III). Samples were taken beneath large mesquite trees, under dense stands of black grama, and in heavy stands of burro-weed.

TABLE III. Effect of burning on some soil constituents and properties of Area B*

Site and treatment	pH	Organic carbon	Total soluble salts	Nitrogen	Potash
		Parts per million			
Under large mesquite					
Before fire	5.8	0.752†	160	20.5	10.0
After fire	5.65	0.590	185	25.0	7.5
Under dense black grama					
Before fire	5.65	0.301	85	10.0	8.0
After fire	5.7	0.657	100	18.0	4.5
In heavy burro-weed					
Before fire	5.7	0.420	375	14.0	13.0
After fire	5.8	0.497	335	14.0	Trace

*Analysis by E. L. Breazeale of the Soils Department, University of Arizona

†Each figure represents mean of 2 samples taken at 2 sites. Each sample composed of top 1 inch of soil from 3 separate local sites.

Nitrogen increased at two sampling sites and showed no change at the other as a result of burning. A similar relation held for total soluble salts, except for the practically bare soil under heavy burro-weed. Burning consistently lowered potash, but effected no appreciable change in pH of the soil. Organic carbon decreased under large mesquites where there was an accumulation of litter and some humus, but increased on the other two sites following burning. Duration of the changes in nutrient content of fresh burns was not studied. However, research by Sampson (1944) in California has shown that the effect of fire on the soil constituents measured is largely nullified by the second year, and disappears in subsequent years.

The June burn laid the area bare just prior to the summer storms, which usually are intense in the region (Fig. 6). As a result, the area appeared very erodible during most of the first growing season. However, no measurements of erosion were made.

SUMMARY

The effects of June burning on two grass-shrub areas in the semidesert grassland type of southern Arizona are reported. Both areas are on the

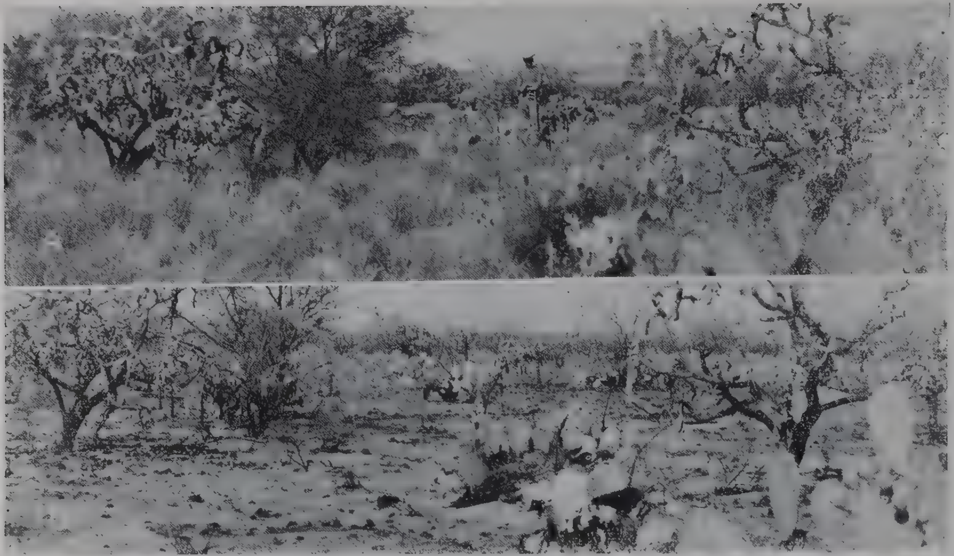

Fig. 6. (A) Character and abundance of vegetation prior to burning for the selected photopoint of Figure 4. (B) Immediately after burning, showing fuel consumption and increased exposure of bare soil to erosive influences.

Santa Rita Experimental Range near Tucson, Arizona. One, about 100 acres, contained an abundance of Rothrock grama, black grama, tangle-head, and a number of perennial three-awns as the predominant perennial grasses. It was lightly to moderately grazed by cattle during the fall and winter months. The other, about 6 acres, ungrazed since 1929, was primarily black grama with some Arizona cotton grass, three-awns, and other species. Burro-weed, cholla, and pricklypear cactus and velvet mesquite were abundant on both areas. The purpose of the study was to determine the effect of broadcast fire on the reduction of both the undesirable shrubs and on the desirable grasses.

Burro-weed was reduced by about nine-tenths, cholla reduced by about half, and pricklypear by about one-fourth by a single burn. Velvet mesquite, the most undesirable shrub, was reduced only by 9 per cent. Of the few mesquite trees killed, all had basal stem diameters less than 6 inches. All trees with stems less than 2 inches were affected by burning but 60 per cent of them sprouted.

Density and herbage production of all perennial grasses were greatly reduced by burning but most recovered by the end of the second to fourth growing seasons. Black grama, one of the most important forage species of the semidesert grassland type, was seriously damaged by burning, and did not recover during the period of study. Burning released some of the soluble salts and nitrogen in the soil.

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ECOLOGICAL STUDIES OF FOREST TREES AT CHALK RIVER, ONTARIO, CANADA

II. ECOLOGICAL CONDITIONS AND RADIAL INCREMENT[1]

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Introduction

This is the second contribution in a series of broad ecological studies of forest trees at Chalk River. The first paper (Fraser 1954) described site types and tree distribution on an 8-acre experimental plot at the Petawawa Forest Experiment Station, Chalk River, Ontario. Attention is now turned to the relation between radial growth of trees and their environment. Information presented includes description of the canopy, air and soil temperatures, rainfall, and soil moisture. Results of studies of radial increment in relation to these physical factors are presented for the period 1949-1953. Special attention is given to growth of yellow birch (*Betula lutea* Michx.) owing to the particular interest in this species as a result of widespread injury in the Maritime Provinces.

Canopy

The measurement of crown closure was undertaken to assist in the understanding of stand climate and particularly points of contrast with similar data recorded in the open. Also, it was considered important to know the condition of the crown canopy each year as a general expression of stand health, and as a possible explanation of differential contrast between physical factors in the open and within the stand in different years.

Since photoelectric cell measurements are not entirely satisfactory for measuring crown closure owing to diurnal and seasonal changes in light condition, the "moosehorn" periscope developed by Robinson (1947) and modified as described below was used in this study. The vertical aperture of this instrument contains a glass plate graticuled into 25 squares. Looking into the eyepiece, the observer views the crown through the vertical aperture by means of a mirror set at a 45-degree angle. The number of squares covered by the foliage is recorded. When held at eye level the grid subtends an area of one milacre at a height of 40 feet. Canopy observations were made at 100 stations, 10 links apart, on each of the 80 square chains of the experimental plot during August when the leaves were fully developed. Although there were variations in height of the canopy from the ground, this intensity of study allowed for approximately 100 per cent crown canopy sampling.

The consistency of crown closure measurements with this instrument was tested by the selection of 33 stations, at each of which one observer made 10 determinations, and three other observers made a single determination. Variability in the records obtained by the single observer was related to the density of the crown canopy. For the stations where the average canopy closure was about 64-76 per cent, the average range within the series of 10 measurements was 20 per cent (*i.e.*, a range of 5 squares on the grid) and the standard deviation of measurement was 4.6 per cent; where the average canopy closure was 80-92 per cent, the average range was 14 per cent, and the standard deviation 3.2 per cent; where the average crown closure was about 92 per cent, the average range was 2.4 per cent, and the standard deviation was 0.8 per cent. Somewhat more consistent readings were obtained by one observer than by the entire group of four observers. At nine of the stations, the single readings of one or more of the last three observers fell outside the range established by the 10 readings of the first observer by one class (4 per cent crown closure), at one station by two classes (8 per cent), and at one station by three classes (12 per cent).

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These results indicate that the "moosehorn" gives quite consistently close readings of crown closure at high crown canopy densities, but less accurate readings at moderate crown canopy densities.

In studying the canopy of the entire plot, observations were made during calm days to avoid difficulties introduced by swaying of the tree crowns. The data were grouped into 5 density classes. The proportion of sampling stations characterized by low crown densities was so small that broad classes of crown density were accepted at the lower ranges, while much narrower classes were used at the high ranges (Table I).

In 1949 and 1950, the crown canopy classifications were very similar, over 90 percent of the plot being placed in the highest crown density class. In 1951, an infestation of the forest tent caterpillar (*Malacosoma disstria* Hbn.) caused moderate defoliation of basswood (*Tilia americana* L.), red oak (*Quercus rubra* L.), and sugar maple (*Acer saccharum* Marsh.), and light defoliation of white birch (*Betula papyrifera* Marsh.). The resultant opening up of the canopy is reflected in the measurement of crown density during 1951 when only 58 per cent of the plot was recorded in the highest crown density class. Less defoliation occurred in 1952 with a corresponding improvement in crown closure. Although there was no defoliation in 1953, the crown closure remained the same as the previous year. The underdevelopment of the crown in 1953 is attributed to lack of stored food caused by decreased photosynthetic capacity during the previous two years of defoliation.

TABLE I. Percentage of plot area corresponding to various crown density classes over a 5-year period

Crown density class (per cent)	1949	1950	1951	1952	1953
90-100	92	90	58	70	72
80-89	6	6	19	21	19
60-79	1	3	16	6	6
40-59	1	1	5	3	2
0-39	0	0	2	0	1

TEMPERATURE

A forest tree is exposed to a series of "temperature regimes" from the microclimate of a root tip where temperature fluctuations are gradual and limited in their range, to that of a twig, where the range in temperature may extend from —40° F. in winter to 100° F. in summer. However, the studies of stand temperatures reported in this paper are restricted to air temperature at the 4-foot level, and to soil temperature at various depths, during the summer season.

On the experimental plot, two hygrothermographs were used for continuous measurement of air temperature and relative humidity. Similar records were made in the open. Of the two instruments located on the plot, one was on the top of a lateral ridge, and the other 26 feet lower in a small valley. Each hygrothermograph was located on a platform 4 feet above the ground, with a roof and appropriate shields to shelter the instrument from rainfall and direct solar radiation.

Soil temperature was measured in two ways. In 1949, pits 2 feet deep were excavated, and minimum thermometers were inserted laterally 12 inches into the side of the covered pit at the 6-, 12-, and 18-inch depths. In 1950, soil temperature was measured with thermistors incorporated in fiberglas soil moisture units (Colman 1948). These units were inserted laterally from the wall of a soil pit, into undisturbed strata at depths ranging from 2 inches to 9 feet. There were 9 stacks of these units located in different moisture regimes (Fraser 1954) in the plot. The daily variations in soil temperature were found to be so small that spot readings (Fig. 1) were accepted as representative of soil temperature.

Air temperatures usually fluctuated considerably during the day, and therefore, with the exception of frost, average temperature was considered more closely related to the tree growth period than maxima and minima. Air temperature readings at the two stations within the plot were within 2° (F.) of one another. Average air temperatures in the open during the June-August period were 1 to 2° above those under the canopy. This relation remained the same during 1951, indicating that the partial defoliation of the canopy in that year was not sufficient to influence air temperatures perceptibly at the 4-foot level within the stand.

Soil temperature readings at the 2-, and 3-inch depths (Fig. 1) fluctuated closely with changes in air temperature, but the temperature at greater depths varied only slighly. At the 9-foot depth the temperature ranged from a minimum of 35° F. in May to a maximum of 50° F. in August. These soil temperature conditions are similar to those observed in northern Europe (Geiger 1950).

There are stated to be two critical temperatures beyond which growth of forest trees is severely liimted. Toumey and Korstian (1947) state that when the mean air temperature during the four hottest months of the growing season falls below

50° F. tree growth is seriously reduced. The upper thermal death point for leaves of many plants is at or near 122° F. (Curtis and Clark 1950), although continuous exposures to 86° F. or above may also result in severe injury or death. Table II shows occurrence of frost in May of each year, and the number of hours, by month, during which temperatures dropped below 50° F. in the open.

TABLE II. Number of May days in which frost occurred and number of hours by month with temperatures below 50° F. in the open at the Petawawa Forest Experiment Station 1949-1953

Year	Number of Days With Frost	Number of Hours Below 50° F.				
	May	May	June	July	Aug.	Sept.
1949.......	6	312	54	14	48	280
1950.......	8	—*	110	24	50	266
1951.......	2	—*	56	4	44	250
1952.......	4	310	56	12	38	174
1953.......	3	254	90	26	74	244

*No records

The influence of contrasting seasonal climates in various years on tree growth, particularly the occurrence of frost in May, and of temperature below 50° F. in June, is discussed in the later section on radial increment studies.

RAINFALL

Six rain gauges were set up in the experimental plot in 1949, three (Nos. 1, 3, 5) along the upper ridge on the west side of the plot, and three (Nos. 2, 4, 6) along the valley floor. In 1950, a seventh gauge was added in the northeast corner of the plot. One rain gauge, located at Station Headquarters 6 miles away, recorded the rainfall in the open. A comparison of the rainfall data from the open and from under the canopy, indicates the amount of rainfall intercepted by the foliage.

Because the leaves on all trees had appeared by June 1, and started to fall by early September, the June-August period may be considered as one of deciduous canopy coverage for the estimate of rainfall penetration (Table III).

The type, duration and intensity of each rainfall may be more critical than the actual amount of rainfall, in relation to penetration through the canopy (Kittredge 1948). The canopy directly above each rain gauge was in the 90-100 per cent crown-closure class with the exception of No. 1 gauge in 1951 and 1953, when the canopy was in the 80-89 per cent crown-closure class. In these two in-

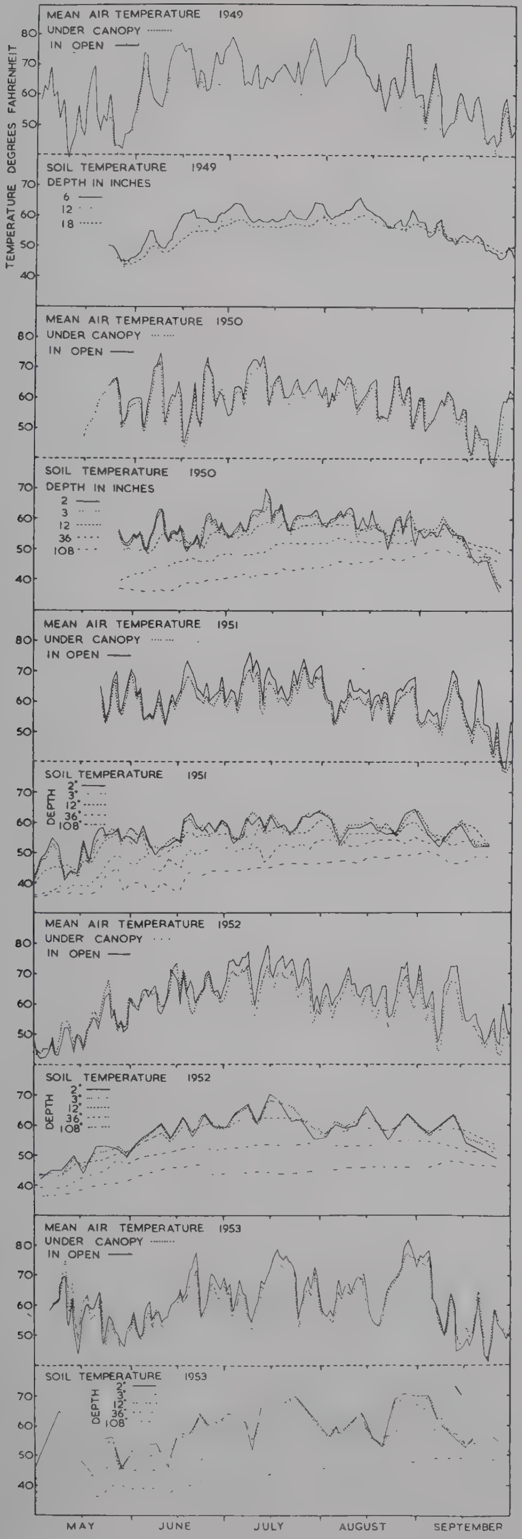

FIG. 1. Summer march of air and soil temperatures on the plot. Air temperatures represent daily mean temperatures based on 2-hourly readings. Soil temperatures represent spot readings taken at 8:00-9:00 a.m.

TABLE III. Rain (inches) as recorded by seven gauges under the canopy and one in the open during June-August, 1949-1953. Percentage of rain penetration through canopy shown in brackets

Guage	1949	1950	1951	1952	1953	Average 1949-53
No. 1...	6.69(77)	10.26(79)	6.37(65)	6.69(73)	4.77(78)	6.96(74)
No. 2...	6.26(72)	9.97(77)	6.28(64)	6.88(75)	5.33(87)	6.94(74)
No. 3...	7.07(82)	10.32(79)	8.24(84)	7.71(84)	5.67(92)	7.80(83)
No. 4...	7.81(90)	14.55(112)	8.98(91)	7.03(77)	5.36(87)	8.75(93)
No. 5...	7.39(85)	11.07(85)	8.51(86)	7.56(83)	5.53(90)	8.01(86)
No. 6...	7.37(85)	12.44(96)	8.21(83)	8.74(96)	5.76(94)	8.50(91)
No. 7...	—	11.69(90)	7.25(74)	7.37(81)	5.04(82)	7.83(82)
Average.	7.10(82)	11.47(88)	7.69(78)	7.43(81)	5.35(87)	—
Open...	8.67	13.01	9.86	9.15	6.15	9.37(100)

stances, the increase in the amount of canopy opening was not reflected in an increased rainfall penetration. Canopy measurements did not evaluate thickness of canopy which would be important in rain interception. Rain reaching the ground through trunk drip was not measured. Rain gauge No. 4 (Table III) showed a penetration greater than 100 per cent in 1950. This may have been due to branch drip which concentrated the rainfall into the area directly over the gauge. Rain gauges Nos. 1 and 2 showed the least rainfall penetration (74 per cent) over the study period. This was possibly due to the very dense hemlock (*Tsuga canadensis* (L.) Carr.) canopy above these gauges.

The driest summer occurred in 1953 when the rainfall was less than half that which occurred in the wet summer of 1950. Differences in total precipitation were reflected in the levels of the water table (Fraser 1954) and soil moisture on different moisture regimes during the period of study.

SOIL MOISTURE

In the first paper of this series (Fraser 1954), the distribution of forest trees in relation to soil moisture sites on the 8-acre experimental plot was described. The plot was divided into soil moisture regimes described by Hills (1945). According to this system the complete range of soil moisture conditions from extremely dry to almost continuously saturated is represented by eleven indices, Θ (theta), 0 to 9. Moisture regimes from moderately dry (1) to very wet (6), are represented on the plot and were recognized through their soil profile development.

Two methods were used to determine seasonal fluctuations in soil moisture. The gravimetric method consists in removing a soil sample from different horizons for determination of water content. It involves collection of many soil samples, and is not suitable for accurately observing the daily changes in soil moisture. This method was used in 1949. The electrometric method involves the measurement of resistance in units placed in the soil. These units consist of two electrodes embedded in gypsum, nylon (Bouyoucos 1949), or fiberglas (Colman and Hendrix 1949). This method was found to be more satisfactory for the conditions studied. From 1950, moisture units of nylon and fiberglas were used to observe periodic changes in soil moisture. The fiberglas units were more suitable for this study than the nylon type, because of greater uniformity in their manufacture and the incorporation of a thermistor for temperature measurements.

The units were placed in vertical stacks, at the 2-, 3-, 6-, 12-, 18-, and 36-inch depths, except on the driest site where the deepest one was at the 108-inch depth. Nine stacks were distributed over the plot, three stacks on each pair of soil moisture regimes. To facilitate measurement of resistance in the soil moisture units, a three-place, seven-gang switch was used for every stack of units. Neoprene-covered three-conductor cable was used between the soil unit and meter connections (via the switch). The individual wires were colour-coded, and a colour group was assigned for each soil-unit lead to avoid confusion at the meter connections. It was important to maintain the identity of each lead from the soil unit, because once the soil unit was buried, the lead terminals were difficult to distinguish. For accurate measurement the soil units need to be in close contact with undisturbed soil. Therefore the units were installed laterally to a distance of at least 12 inches from the side of an auger hole or pit. The longitudinal axis of the unit was placed parallel to the movement of gravitational water.

The resistance of the electrode sandwich varies with the temperature as well as soil moisture. For this reason, it is necessary to convert resistance measured at field temperatures to the resistance that would have been measured at some standard temperature. Colman (1948) recommends 60° F. as the standard temperature, and he has devised a temperature correlation chart based on laboratory studies with soils representing a wide range in texture. His graphs were used in standardizing the readings.

In the loamy sand from the plot, a saturated condition is represented by a resistance of 250 ohms, field capacity by 800 ohms, and the wilting point by approximately 100,000 ohms. The wilting point represents the amount of water left in the soil when the plant is permanently wilted, that is, when the plant will not regain turgidity when exposed to a saturated atmosphere (Weaver and Clements 1938). The units were calibrated by growing sunflower seedlings in glass jars filled

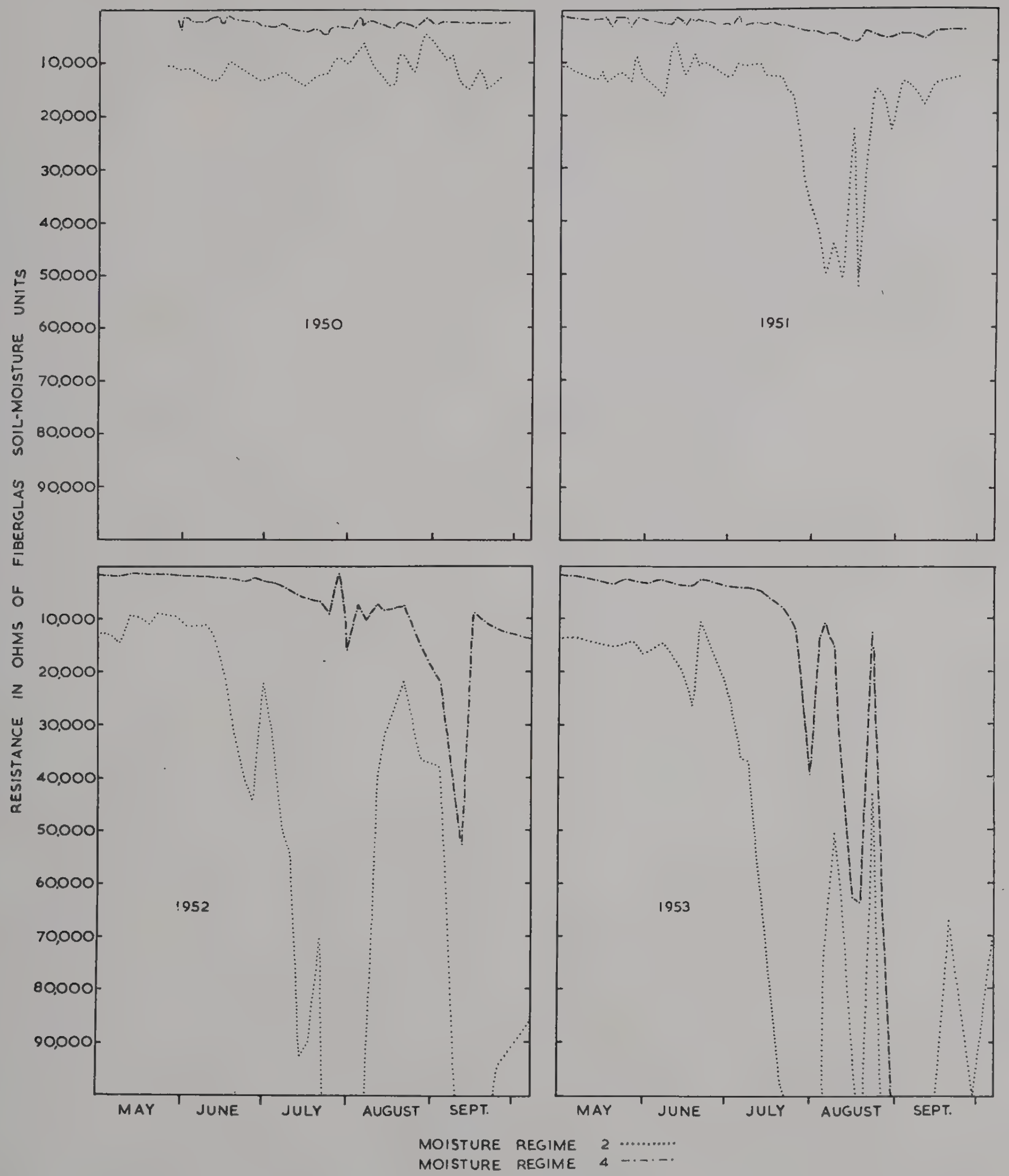

FIG. 2. Summer march of soil moisture in the upper 36 inches of soil as measured with fiberglas soil units on two sites.

with soil from the plot. A fiberglas unit was placed in each jar. When the sunflowers were about 6 inches high, the surface of the soil was sealed with wax. The resistance of the unit was then observed periodically until the plant showed permanent wilting. Additional experiments using tree seedlings instead of sunflowers are now in progress and will be reported in a later contribution.

The soil moisture conditions (Fig. 2) in the upper 36 inches of the soil on moisture regimes 2 (dry) and 4 (wet) of the plot, represent averages from three soil moisture units at the 3-, 12-, and 36-inch depths. The lower the curve, the drier the soil.

In 1952, wilting conditions were first apparent on moisture regime 2 from the last week of July to early August, and again in mid-September. In

1953, wilting conditions occurred on moisture regime 2 from July 22 to August 5, and again on both sites from August 28 to September 16. The effect of this drought was apparent in reduced radial increment (Figs. 3, 4, 5). A number of broadleaved trees were wilted during this drought. Details of changes in soil moisture at different depths following rainfall at various times of the year will be considered in a separate contribution.

RADIAL INCREMENT

Initiation of cambial activity of forest trees in the spring is considered to be triggered by a growth hormone from developing buds (Jost 1891, Wareing 1951, Fraser 1952), but total radial growth appears to be regulated by environmental factors such as temperature or moisture, which impose limiting conditions. In view of Priestley's suggestion (1930) that frost may be the cause of seasonal interruption of cambial growth in American trees, it is of interest to ascertain as closely as possible the time when initiation and cessation of cambial cell division take place. An estimation of these dates can be based either on anatomical study of cores removed from the tree at intervals throughout the seasons, or on dendrometer readings. The type of dendrometer used was that developed by Belyea, Fraser, and Rose (1951), which utilizes a standard dial gauge graduated in thousandths of inches, and which is mounted on a triangular base. Through an aperture in the center of the base projects a movable spindle. From the angles of the base, three pointed legs project downward. When the instrument is in use, the three legs are applied to the heads of three screws which are permanently inserted deep into the wood of the tree, while the movable spindle impinges on the flat head of a thumb tack glued to the bark. In this manner any radial increment is registered in the dial gauge by differences in readings.

For the study of radial growth, 30 yellow birch trees and 4 representatives of each of the other abundant species, were selected in different parts of the plot. Frequent dendrometer readings were made on the south side of the trunk 4 feet above the ground. Throughout the summer of 1950, cores from one tree of each species were taken periodically with a cutting tube, for microscopic study. In this procedure, use was made of a steel cutting tube which consists of a ¾-inch hardened steel pipe ground to a sharp chisel edge at one end. After the outer part of the dead periderm had been carefully chipped away, the cutting tube was driven in to delimit the segment. A chisel was then inserted beside the cutting tube and served as a lever to ensure that the delimited segment was removed from the tree with the tube. The segment was pressed out of the tube by means of a wooden rod. It was then trimmed, labelled, and preserved in 70% alcohol and glycerine in equal proportions. Radial sections were later cut on a sliding microtome. The samples were taken at the same level as the dendrometer reference points. These anatomical examinations assisted in the evaluation of the dendrometer data. Neither method gives a completely accurate picture. The dendrometer merely records total radial increment changes without distinguishing changes caused by cell division and swelling whereas the sectioning method has a number of limitations. Each sample taken leaves a wound which may affect subsequent growth and successive samples cannot be taken from the same portion with the result that the variations in the amount of cambial growth on different sides of the tree complicates the results. Dendrometer readings were taken between 8 and 9 A.M. to minimize error caused by diurnal fluctuations of temperature and moisture.

The number of undifferentiated cells in the cambial zone increases two- to three-fold when the cambium is most active, and decreases to a constant number at the end of the growing season. Constancy in number of undifferentiated cells coincides with a comparative constancy of dendrometer readings at the end of the growing season. By comparing the results of anatomical samplings early in the season with corresponding dendrometer readings, a swelling is invariably found before any wood cells have been laid down. After the initial lag, the radial increment curve assumes a sharp upward rise marking the period of active cell division in the cambium. Near the end of the season, usually in August, a third phase is delimited when the slope of the curve becomes very slight. The increment during this last phase rarely amounts to more than one or two mils (thousandths of an inch), and probably represents final maturation of differentiating tissue. That the more vertical part of the curve represents the period of cambial activity has been borne out by a study of all sectional material available. In most instances the line of demarcation between these phases is quite distinct; however, where the total amount of radial increment is relatively small, the change in slope of the curve is gradual, making the separation of the different growth phases more difficult.

Table IV summarizes radial growth data obtained from one tree of each species studied in 1950.

Column (2) shows increment from May 12 to

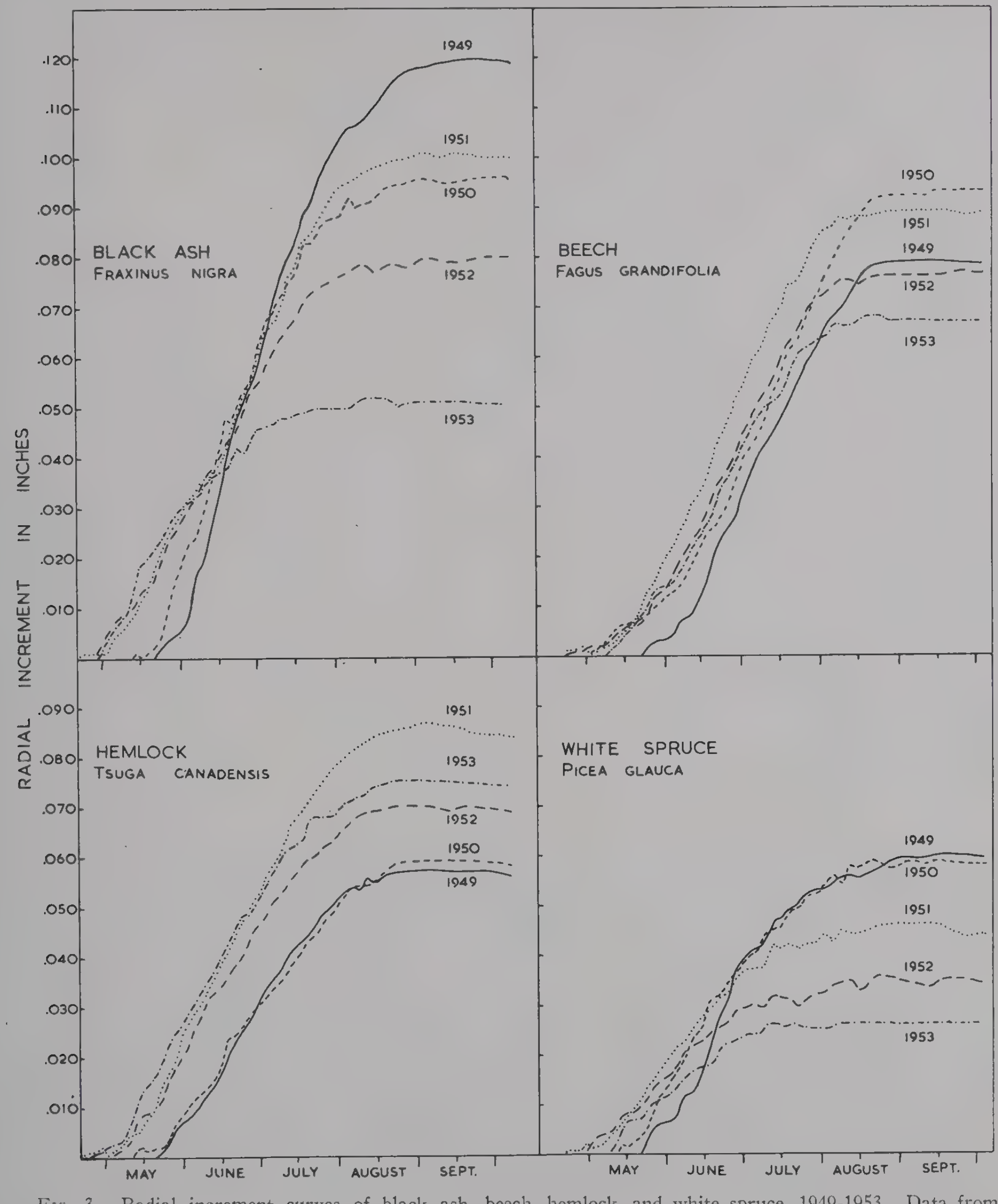

Fig. 3. Radial increment curves of black ash, beech, hemlock, and white spruce, 1949-1953. Data from averages of four trees of each species.

October 13, 1950, as measured by the dendrometer. The xylem recorded in column (3) was measured in the cores, and column (4) represents the difference between the two. Column (5) represents the difference between readings taken February 1, 1951, and those on October 13, 1950. Columns (6), (7), and (8) present at good illustration of the difficulties connected with studying radial increment by the sampling method, for in only two of the eight species could these columns be completely filled, despite the exercise of greatest care to avoid injury to the delicate tissues. Columns (9) to (12) include the estimated dates for the beginning and ending of cambial cell division. Here also the results obtained from the sectioning of cores are disappointing for only in two trees did

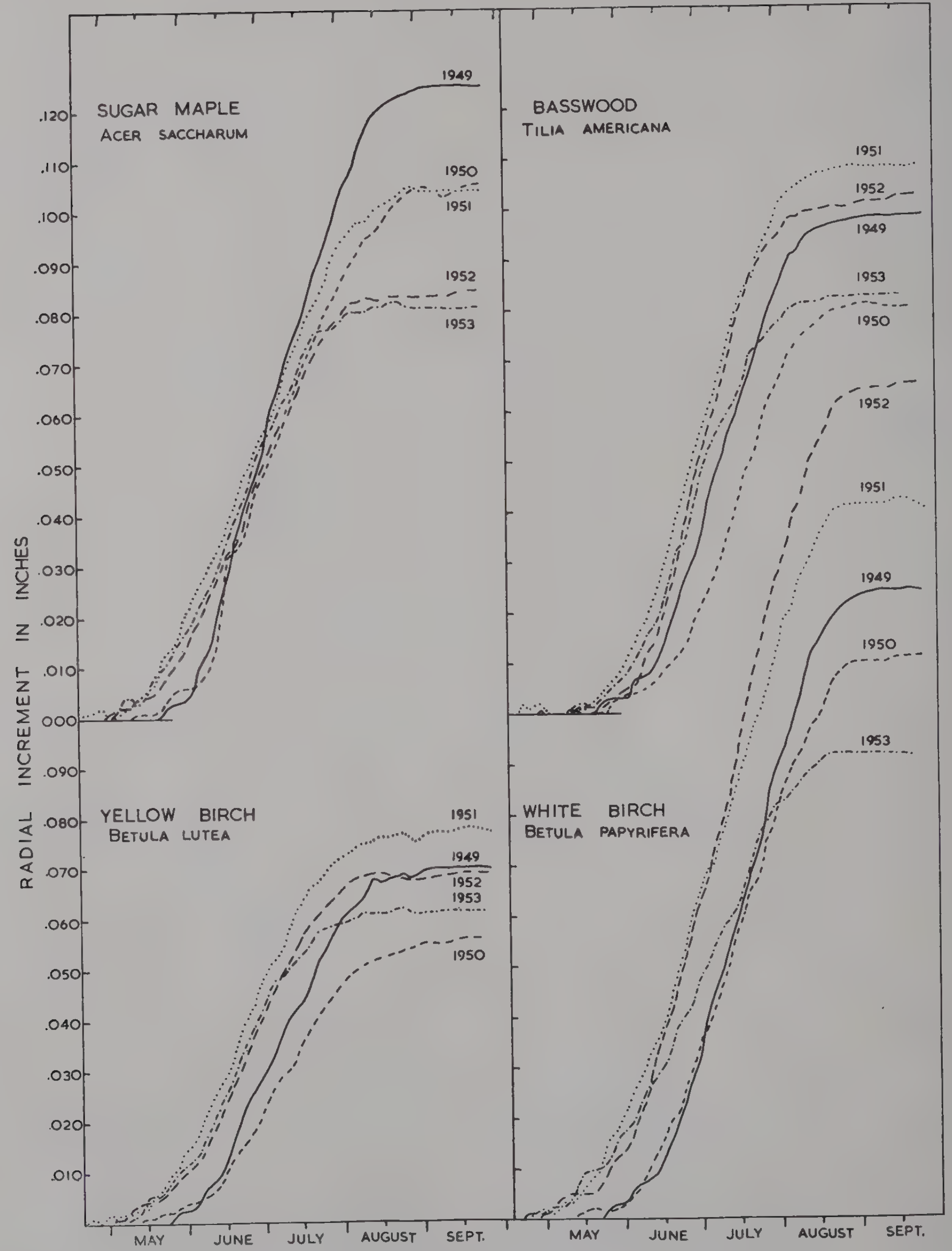

Fig. 4. Radial increment curves of sugar maple,basswood, yellow and white birch, 1949-1953. Data from averages of four trees except for yellow birch where 30 trees were used.

the cambial zone remain intact in all the samples. Even with these trees only an estimate can be made because of the intervals between sampling. Where complete cores were not available, a growth initiation estimate based on the development of new xylem could be obtained, because this tissue

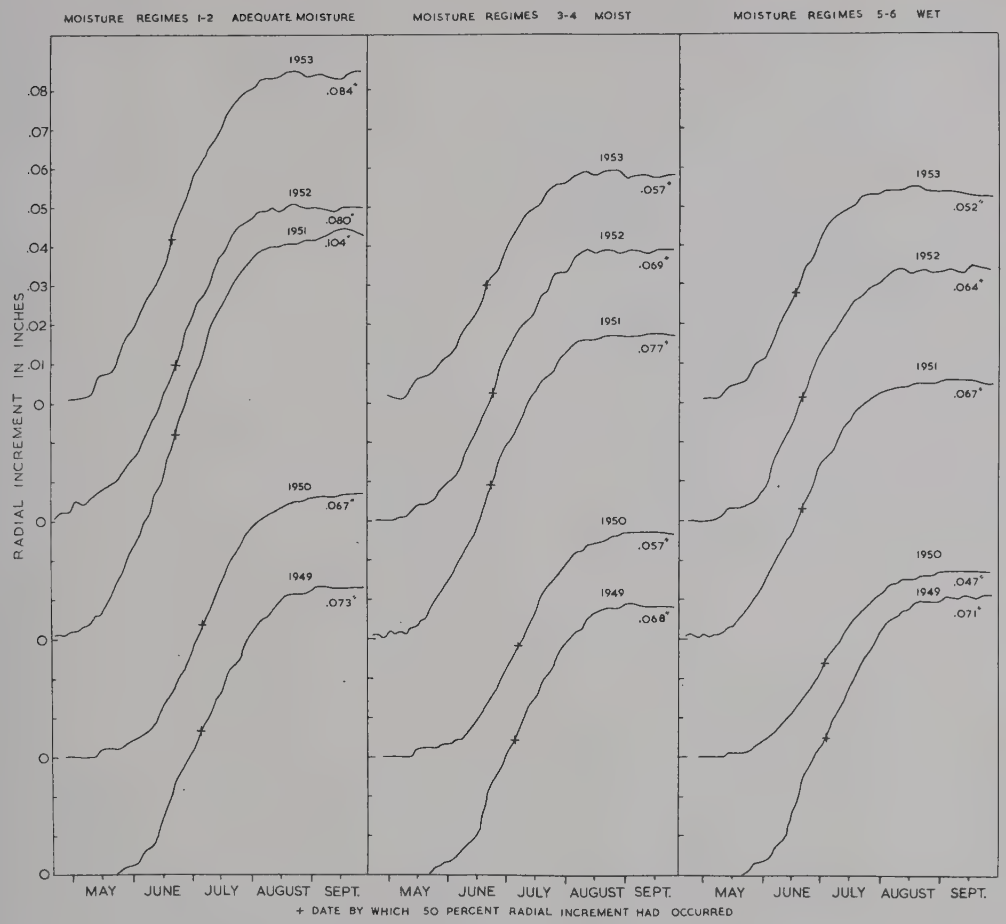

FIG. 5. Radial increment curves of yellow birch on three sites. Data from averages of five trees on moisture regimes 1-2; 14 trees on moisture regimes 3-4; and 11 trees on moisture regimes 5-6.

is formed before the phloem (Brown 1912). For deciding the time of cessation of growth, similar treatment is impossible since there is no way of knowing by inspection of the sieve cells whether a particular one is or is not, the last cell formed for the season. But when sufficient numbers of uninjured samples are available, it can be estimated when the minimum thickness of the cambium layer is reached in autumn. Such cessation estimates coincide with those obtained with the dendrometer.

In black ash (*Fraxinus nigra* Marsh.) No. 15, the formation of wood (xylem) for 1950 was well begun by the time the first core was taken on June 4, but the cells of the cambial zone were so fragile that they were always crushed during sampling, and no satisfactory record of the cambial cells or the sieve cells was obtained. Black ash has a ring-porous wood. Four layers of vessels were produced by June 15, and the same number was found in every subsequent sample. The production of fibre tracheids seems to have stopped by July 22, although the cambium was probably active for some time after this, since this region was still very fragile until September 5. The estimated thickness of the annual ring in the wood was 70.2 mils. The shrinkage from October, 1950, to February, 1951, was 20.3 mils which was very close to the original thickening the previous spring.

Initial wood deposition for beech (*Fagus grandifolia* Ehrh.) No. 4, began between June 4 and June 15. By the latter date, 5 vessels, intermixed with 6 fibres, had been produced. Thickening of the cambial zone prior to this accounted for 4.9 mils. Growth ended about August 20, after which only slight differences in dendrometer readings were recorded. Radial growth of beech

TABLE IV. Anatomical and dendrometrical measurements of radial growth of eight trees at Chalk River in 1950

Species	INCREMENT IN THOUSANDTHS OF INCHES (Mils)				LAYERS OF CELLS IN CAMBIAL ZONE			DATES OF CAMBIAL CELL DIVISION			
								Initiation Estimated from		Cessation Estimated from	
	Total	Xylem	Phloem Periderm Swelling	Loss of Increment Oct. 1950-Feb. 1951	Spring min.	max.	Fall min.	Sections	Dendrometer	Sections	Dendrometer
(1)*	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
Black ash No. 15	143.7	70.2	73.5	20.3	—**	—	—	2 vessels by June 4	May 21		Aug. 20
Beech No. 4	100.4	73.6	26.8	6.9	—	9	4	Camb. swollen June 4, 5 vessels & 6 fibres by June 15	June 2	Aug. 20	Aug. 20
Hemlock No. 2	39.4	27.6	11.8	18.7	7	16	3	2 Tracheids by June 4	May 24	Aug. 20	Aug. 20
White spruce No. 1	42.3	6.6	35.7	13.8	—	9	3	9 Camb. initials by June 4	May 23	Aug. 5	Aug. 5
Sugar maple No. 38	109.4	76.6	32.8	8.9	—	6	—	3 vessels & 12 fibres by June 4	May 21		Aug. 20
Basswood No. 37	107.3	106.3	1.0	30.5	5	17	—	1 vessel by June 23	June 13		Aug. 21
Yellow birch No. 6	17.7	10.6	7.1	21.6	3	7	3	7 Camb. initials & 1 vessel by June 23	June 9	Aug. 13	Aug. 5
White birch No. 8	127.6	78.7	48.9	15.7	—	10	5	1 vessel & 5 fibres by June 15	June 10		Aug. 28

*Columns numbered for text reference. **Cells damaged in sampling.

(Fig. 3) usually started at the end of April or early in May, and extended to early August. In 1949, dendrometer measurments were not started until May 23, and from the shape of the curve, radial growth appeared to have started by that time. Shrinkage from October, 1950, to February, 1951, was 6.9 mils.

Similar data for hemlock No. 2 show that two layers of tracheids were formed at the 4-foot level by the first sampling on June 4, 1950, when the dendrometer readings indicated an increment of 10.8 mils. Since the two layers of tracheids present had a total width of 3.3 mils, the amount caused by swelling was 7.5 mils. The 7 layers of sieve cells present in this sample appeared to have been developed the previous season. The number of undifferentiated cells in the cambial zone during the active growing season in June was about 16, decreasing gradually as growth slowed down in late July when summer wood formation started. By the end of August, when increment had ceased, there were only 3 layers of undifferentiated cells in the cambial zone. The thickness of the 1950 annual ring of wood was 27.6 mils, whereas the corresponding radial increment, as measured with the dendrometer, was 39.4 mils, thus leaving 11.8 mils attributed to bark. A reading taken on February 1, 1951, showed a shrinkage of 18.7 mils. The effect of the drought in mid-July 1953 is apparent in the more irregular shape of the curve at this period. Growth was not reduced by the drought, owing to the location of the trees on the wetter site. The greater amount of growth during 1951, 1952, 1953 is attributed to an earlier initiation of radial increment.

In white spruce (*Picea glauca* (Moench) Voss) No. 1, the first spring tracheids from the 4-foot level of the trunk were observed on June 23, 1950, although 4 layers of spring tracheids were found in twigs as early as June 15. At this time, a swelling of 19.7 mils was recorded in the trunk by the dendrometer. The 9 layers of undistorted sieve cells present in these samples appeared to have developed during the previous growing season. The number of layers of undifferentiated cells in the cambial zone during the growing season was 8 or 9, decreasing gradually as growth slowed down in July, until by August, when radial increment had practically ceased, it had diminished to 3 layers. The complete annual ring in 1950 was 6.6 mils thick. The total radial increment measured by the dendrometer was 42.3 mils, leaving 35.7 mils attributable to swelling and addition of new tissue other than wood. This spruce tree appeared to be decadent, as indicated by poor foliage, and it was apparent that the foodstuffs elaborated in the declining tree were channelled into new bark tissue rather than wood, as is usual in healthy individuals. The average growth data also indicated a continuous decline in vigour.

Growth records for sugar maple No. 38 show that new wood formation had started by the time the first sampling as made on June 4. Three layers of vessels, intermixed with 12 fibers having a total width of 13.4 mils, corresponded to dendrometer reading of 18.7 mils, thus indicating at this stage a thickness of 5.3 mils attributable to bark and cambial swelling. The cambium was particularly fragile so that records were not obtained for the number of cells in the cambial zone at different periods of its growth. The width of the annual ring for this maple was 76.6 mils. The amount of radial increment less 5.3 mils caused by the initial thickening of the cambial zone, was 104.1 mils, leaving 27.1 mils to be made up of phloem and periderm. The subsequent contraction, as indicated by the reading of February 1, 1951, was 8.9 mils. The response in radial growth of sugar maple to climatic fluctuations was somewhat different from that of other species. In spite of a later initiation of growth in 1949 and 1950, the rate of growth during these two years surpassed that of the other years.

In basswood No. 37, the first new wood was not observed until June 23, when the amount of thickening in the cambial zone was 6.6 mils. Secondary growth ended August 21. Radial growth curves of basswood indicate a rather late initiation of cambial activity. The onset of the steep part of the curve marking first cell division did not usually occur until early June, and there was not much spread in the time of initiation of growth over the study period. Since this species is, at Chalk River, near the northern limit of its range its late development would favour survival by escaping damage from late spring frosts.

In white birch No. 8, new wood deposition was initiated between June 4 and June 15, 1950. The cambial region was so delicate that few records of cambial initials could be obtained, but sections in different samples showed 10 layers, whereas the number had been reduced to 5 by September 5. Dendrometer readings showed that radial increment ended on August 28. Shrinkage of bark and cambium amounted to 15.7 mils by February 1, 1951. White birch showed a differential growth response to variations in climatic conditions with its greatest growth in 1951 and 1952. Growth was reduced by climatic extremes as shown in the decreased increment in the wet year of 1950 and the very dry year of 1953. In general, white birch had a greater amount of radial growth than any other species studied.

In yellow birch No. 6, the production of wood began between June 15 and June 23, 1950, and apparently ended by August 13. The thickness of the annual ring produced during that time was 11.4 mils. The radial increment as measured with the dendrometer was 17.7 mils. The number of cambial initials varied from 7 at the peak of growth to 3 in the dormant period.

The radial increment curves (Figs. 3 and 4) represent characteristic growth patterns of the 8 species studied as well as seasonal variations of radial growth over the five-year period. In addition, the study of a larger number of yellow birch shows the effect of site variations on radial growth of this particular species (Fig. 5). The crown condition of the yellow birch trees whose growth is illustrated in Fig. 5 and summarized in Table V, either improved or remained the same during the period of study.

Table V also shows the dates of initiation and cessation of radial growth (when 5% and 95% of radial increment had occurred) for yellow birch on 3 soil moisture sites, and for the 7 other tree species studied. The initiation of cambial activity

TABLE V. Time of initiation and cessation of radial incremement, and total radial growth of eight tree species, 1949-1953

Species	1949			1950			1951			1952			1953		
	Init.	Cess.	Total	Init.	Cess.	Total	Init.	Cess.	Total	Init.	Cess.	Total	Init.	Cess.	Total
Yellow birch on															
Site I-II......	—*	Aug. 8	73†	June 3	Aug. 5	67	May 11	July 30	104	May 9	July 25	80	May 14	July 27	84
III-IV......	—	" 8	68	" 3	" 5	57	" 17	" 30	77	" 23	" 25	69	" 14	" 27	57
V-VI......	—	" 8	71	" 9	" 5	47	" 19	" 30	67	" 27	" 25	64	" 21	" 27	52
Black ash......	—	Aug. 17	120	May 21	Aug. 20	96	May 9	July 29	101	May 6	July 29	80	May 8	July 29	52
Beech.........	—	Aug. 14	78	June 2	Aug. 20	93	May 16	July 29	89	May 23	July 29	77	May 21	July 23	68
Hemlock.......	—	Aug. 14	57	May 24	Aug. 20	59	May 13	Aug. 5	87	May 13	Aug. 1	72	May 14	July 20	75
White spruce...	—	Aug. 8	60	May 23	Aug. 5	59	May 13	July 8	47	May 20	July 27	36	May 25	July 1	24
Sugar maple....	—	Aug. 14	125	May 21	Aug. 20	105	May 16	Aug. 8	105	May 23	Aug. 1	84	May 21	July 30	82
Basswood......	—	Aug. 11	98	June 13	Aug. 21	80	May 27	Aug. 8	108	June 6	Aug. 5	103	May 28	Aug. 3	82
White birch....	—	Aug. 20	124	June 10	Aug. 28	111	May 16	Aug. 20	142	May 23	Aug. 15	165	May 14	Aug. 3	92

*Initiation missed †Total radial increment in mils, average of 4 trees except for yellow birch of yellow birch showed considerable variation on different sites and from year to year. Records were not commenced early enough in 1949 to give a valid date of cambial initiation for that year. Radial growth usually started one to two weeks earlier in yellow birch trees on site I-II which had a thin organic horizon. The wetter site V-VI, with its 12-inch "insulating" organic layer, had a delayed spring warm-up of the soil. The year-to-year variation in the initiation of growth in yellow birch amounted to several weeks. Earlier initiation reflected warmer vernal temperatures (Fig. 1). Cessation of radial growth in yellow birch usually occurred around August 1 when neither temperature nor moisture were limiting factors. The average radial growth was greatest in those yellow birch trees located on the sites with optimum moisture and least on sites with more than adequate moisture. Radial growth of all yellow birch was greatly reduced during the very wet year of 1950. The high water table on the wetter sites may have been instrumental in reducing radial growth through poor aeration of the roots which would influence uptake of nutrients.

Black ash had the earliest radial growth which usually occurred during the first week of May (Table V). Basswood was the last to start, almost a month later. Cessation of growth, in most species, occurred in late July or early August. Average radial growth was greatest in those years with warmer vernal temperatures and consequently earlier initiation of cambial activity.

Discussion

The investigations at Chalk River indicate interrelations between tree growth, site, and climatic variations. The time of initiation of growth is considered to be controlled by winter and early spring temperatures. The soil at this time of the year at Chalk River always has sufficient water for growth. On wet sites, a thick organic horizon delays the spring warm-up of the soil, and this may retard initiation of growth. Cessation of growth appears to be regulated by a shortened photoperiod acting through a growth hormone mechanism. Radial growth, which in some species may continue into late August, slowed down quite independently of early autumn frosts. This is in agreement with observations on tree growth by Daubenmire (1949), Daubenmire and Deters (1947), and Eggler (1955). That the control of radial growth is of a hormonal nature is evinced by the continued production of spring wood when b-indole acetic acid is applied in late summer (Fraser 1949). This coincides with the postulations of Jost (1890) and MacDougal (1936) who considered a hormonal stimulus as the internal controlling factor of cambial activity. No distinct change of slope occurred in growth curves of ring-porous species, such as black ash, when the transition from vessel to fibre tracheid took place. This might indicate that a regulating mechanism other than food is controlling cell differentiation. The diffuse porous trees are considered to be more sensitive towards the increase of temperature in the spring (Ladefoged 1952).

MacDougal (1936) considers the period of growth in trees to be imposed by environmental conditions. Lodewick's study (1928) of yellow birch in New York State, several degrees of latitude south of Chalk River, indicated that this species had a longer growing season in that latitude. The growth period is even longer in warmer regions when sufficient soil water is available (MacDougal 1936). The effect of climatic variations on tree growth has long been recognized as shown in a review by Mikola (1952), but compartively little work has been carried out on Canadian forest trees. Duff and Nolan (1953) appreciated growth variations on different sites but no attempt was made to evaluate the factors involved. The present study placed special emphasis on yellow birch because the vigour of this species in eastern Canada had seriously declined over the past few decades. There has been a general recovery in the condition of yellow birch at Chalk River since 1949, although the drought of 1953 was associated with a reduction of radial growth. The recent improvement in health of birch is in agreement with birch conditions in other parts of Ontario (Hill and Sinclair 1954), and Quebec (Pomerleau 1953).

Summary

The annual variations in canopy, air and soil temperature, rainfall, and soil moisture are described for 3 sites of an 8-acre plot at Chalk River, for the 1949-1953 period. Correlations are made between these data and the radial growth of 8 forest tree species. Cambial activity at the 4-foot level in these trees was investigated by sectioning of samples of bark and outer wood, and by the periodic measurements of radial increment with a dial gauge dendrometer. The number of layers of undifferentiated cells in the cambial zone is a reliable index of the current rate of cambial activity, and when a constant minimum number of layers is reached, the radial growth had ceased. The dendrometer readings become constant at the same time.

The time of initiation of growth appeared to be controlled by late winter and early spring tem-

peratures since the soil, at this time of the year at Chalk River, had always sufficient moisture for growth. On wet sites, a thick organic horizon delays the spring warm-up of the soil which consequently retards initiation of growth. Cambial activity in the stem of all trees studied had ceased by early September even on sites where neither moisture nor temperature were limiting.

Acknowledgments

I wish to acknowledge indebtedness to M. L. Prebble, R. M. Belyea, and other colleagues of the Forest Biology Division, and E. E. Gaertner of the Petawawa Forest Experiment Station, for suggestions and criticisms in preparation of the manuscript. I am indebted to Mrs. Evelyn Douglas of the Forest Insect Laboratory, Sault Ste. Marie, for assistance in compilation of the data. D. A. Macdonald, Director of the Forestry Branch, approved the continuation of the study after transfer of the author to that organization in 1953.

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THE EFFECT OF GRAZING INTENSITY ON PLANT COMPOSITION, VIGOR, AND GROWTH OF PINE-BUNCHGRASS RANGES IN CENTRAL COLORADO

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Introduction

What happens to individual forage plants when subjected to different degrees of grazing by cattle? In what way does grazing change growth habits and composition of the herbaceous vegetation? Answers to these basic questions will help the range operator to properly evaluate his range-management practices.

Six experimental pastures on native ponderosa pine-bunchgrass range at the Manitou Experimental Forest near Woodland Park, Colorado, furnished an excellent opportunity to study changes in native vegetation is relation to past grazing use. These units had been grazed at 3 intensities for 9 years. In each unit, exclosures, which had not been grazed for 10 years, were available.

Description of the Area

The pastures are located on alluvial granitic soils in the Trout Creek Valley. These soils are relatively infertile, low in organic matter, and highly erosive. The gently rolling topography has an average easterly aspect with slopes of 10 to 20 per cent. The area is covered with a typical open stand of ponderosa pine (*Pinus ponderosa*)[2] interspersed with grassland parks.

Climatic records at the experimental forest headquarters from 1937 to 1950 show an average annual rainfall of 15.98 inches, with fluctuations ranging from 7.99 inches in 1939, to 25.80 inches in 1947. More than three-fourths of the total precipitation comes during the period of April through September. Normally winters are open with little snowfall. Summer daytime temperatures range from 75° to 85° F. and fall to 35° to 45° F. at night. Winter temperatures average about 40° F. in the daytime and 0° to 5° F. at night.

Methods

Beginning in 1941, the 6 pastures were grazed by yearling heifers from June 1 to October 31, at 3 rates of stocking. The heavy rate was established at 50 per cent or more utilization of the palatable grass and sedge herbage; the moderate rate at 30 to 40 per cent utilization; and the light rate at 10 to 20 per cent utilization. These rates of grazing were not achieved in the beginning. The light intensity was first achieved in 1942, the moderate rate in 1942 on one pasture and in 1943 on the other, and the heavy rate in 1943 on one pasture and in 1944 on the other. After these dates, the utilization goals were achieved each year.

The current study was conducted during 1949 and 1950, and was based on measurements and observations made at 12 locations in the grassland parks of the pastures. Three sites each year were studied on areas typical of the heavy, moderate, and light rates of grazing and 3 sites were in exclosures that had not been grazed since 1939. New sites were selected each year, the sites being protected from grazing by temporary wire exclosures during the year the observations were made. Although not grazed during the year measurements were made, plants in the heavily grazed pastures are referred to as "heavily grazed"; those in moderately grazed pastures, "moderately grazed"; and those in lightly grazed pastures, "lightly grazed."

A series of 20 sampling plots, each 1 foot wide and 10 feet long, was established within each exclosure in the pastures. Random selection of 10 out of each 20 plots determined the actual plot location. Species segregation on each plot was as follows:

Grasses:
- Little bluestem (*Andropogon scoparius*)
- Blue grama (*Bouteloua gracilis*)
- Parry oatgrass (*Danthonia parryi*)
- Arizona fescue (*Festuca arizonica*)
- Mountain muhly (*Muhlenbergia montana*)
- Other grasses

Grasslike:
- Sedges and rushes (*Carex* spp. and *Juncus* spp.)

Weeds:
- Rose pussytoes (*Antennaria rosea*)
- Nickleaf milkvetch (*Astragalus goniatus*)
- Trailing fleabane (*Erigeron flagellaris*)
- Fringed sagebrush (*Artemisia frigida*)
- Other weeds

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[1] Forest Service, U. S. Department of Agriculture, with general headquarters at Colorado A. & M. College, Fort Collins, Colorado.

[2] Nomenclature of plants in this article is based on Standardized Plant Names, second edtion, by H. P. Kelsey and W. A. Dayton.

On each sample plot, the average height growth; number of seedstalks of grasses; number of seedlings; number of plants and number of tufts per plant for grasses;[3] herbage yield; and litter accumulation were determined for each species. In addition, the air-dry weight of roots in the top cubic foot of soil was determined for three major grasses and soil moisture was determined at monthly intervals on each sampling area.

To determine when and to what extent cattle graze the major forage species, 30 grazed plots in each of the 3 pastures were measured in 1950. Percentage composition of the herbage by volume was estimated at the beginning of the grazing season. Utilization by species was estimated on July 18, August 15, and near the end of the grazing season, September 25.

RESULTS

Other investigators have shown that heavy grazing of pine bunchgrass ranges tends to remove the more palatable, high-producing grasses from the vegetational complex (Hanson 1924, Costello and Schwan 1946). These are replaced by grasses of lower palatability, usually sod-forming species, and by unpalatable weeds and half-shrubs. Under the heavy rate of stocking, which brought about the most range deterioration, such deterioration had progressed only to the transition from bunchgrasses to sod grass stages (Johnson 1953). The changes brought about by grazing evaluated here are representative of only first stages of retrogression from the climax conditions. Such changes are the first indications that management practices are at fault and that corrective measures are needed.

Utilization of herbage

The palatable species considered in utilization estimates and their percentage utilization are shown in Figure 1. All species received substantial utilization on the heavy-use areas, but on moderate- and light-use areas, blue grama and fringed sagebrush were only lightly grazed. Mountain muhly and Arizona fescue were grazed most heavily on all except the light-use areas where little

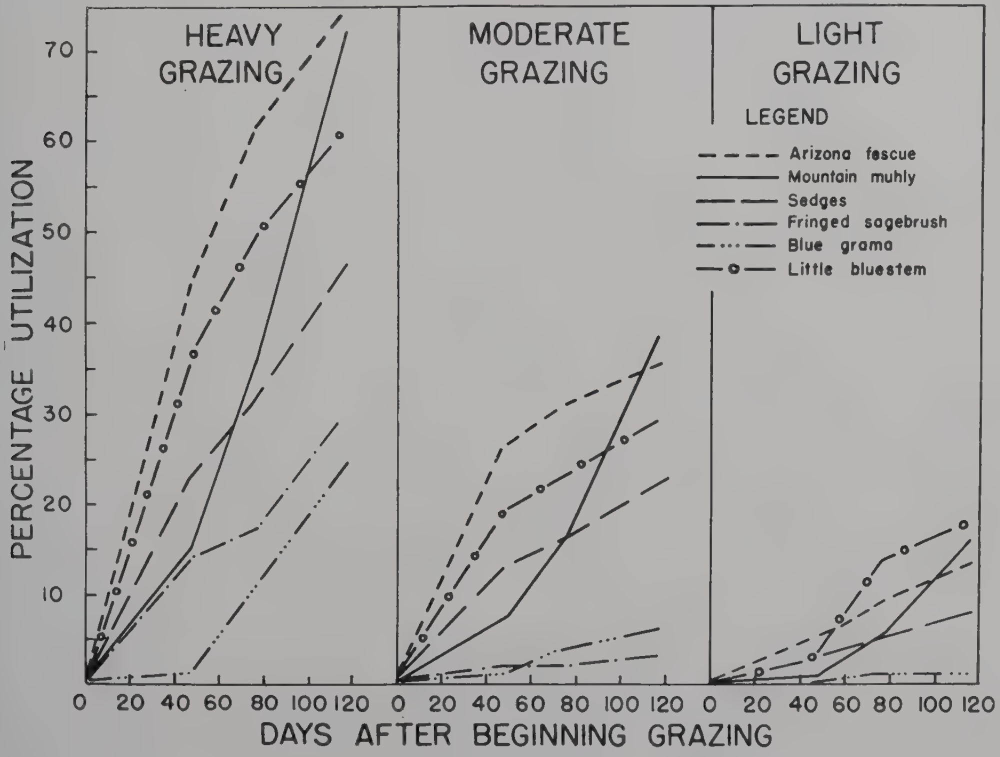

FIG. 1. Seasonal use of major forage species on pine bunchgrass ranges grazed at 3 intensities, Manitou Experimental Forest, 1950.

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[3] A tuft was considered as a part of the crown producing green herbage but separated from other producing parts by one-half inch or more of nonproducing crown.

bluestem received heavier utilization than any other species. Arizona fescue and little bluestem were preferred grasses during the early part of the season. Mountain muhly and blue grama, where they were grazed, received heavier use during the latter part of the season. Sedges appeared to be palatable during all the grazing season. The comparatively light utilization of blue grama and fringed sagebrush, even on areas heavily grazed, explains the ability of these species to maintain themselves and, as the better forage plants are killed, to become the dominant vegetation on overgrazed ponderosa pine-bunchgrass ranges.

Mountain muhly was the most abundant species on all grazing areas studied. Similarly, it furnished the bulk of the forage consumed by cattle. In proportion to the amount of herbage taken, more mountain muhly was grazed on light than on either moderate- or heavy-use areas. On moderate-use areas, where Arizona fescue and mountain muhly were about equal in abundance, they made up about the same percentage of the forage consumed. Heavy grazing was the only degree of use under which blue grama furnished any appreciable volume of forage.

From these studies, it appears that both palatabality and abundance are importance in the way cattle graze the vegetation. Palatability determines the degree of utilization of the species. Little bluestem and sedge were comparatively heavily utilized under all rates of grazing, but never furnished any appreciable volume of forage because they were not abundant. Some species such as blue grama and fringed sagebrush were fairly abundant on the heavily grazed areas, but were not heavily utilized. They were grazed only after the more palatable species were heavily utilized.

Species composition

On heavily grazed areas, the grasses and sedges, based on air-dry weight of total herbage, made up an average of 48 per cent of the composition (Table I). On moderately grazed areas, grasses and sedges comprised 70 per cent, and on light- and non-use areas 75 per cent of the herbage.

Mountain muhly and Arizona fescue occurred with the least frequency on heavily grazed areas. Arizona fescue, a grass palatable in the spring and early summer, contributed little to the herbage produced on heavily grazed areas but was most abundant on those moderately grazed. It was not so abundant on ungrazed and lightly grazed areas as on those moderately grazed. Mountain muhly produced more herbage than other species, except on moderately grazed areas, and it formed an increasingly larger percentage of composition as the intensity of grazing use was reduced. It varied from an average of 20 per cent of the composition on heavily grazed areas to 45 per cent on those not grazed.

Blue grama occurred on all except a few of the plots in lightly grazed areas. It was most abundant on areas heavily grazed, and on these areas,

TABLE I. Species composition based on herbage yield, Manitou Experimental Forest—1949, 1950

Species	PAST GRAZING TREATMENT											
	Heavy			Moderate			Light			None		
	1949	1950	Ave.	1949	1950	Ave.	1949	1950	Ave.	1949	1950	Ave.
	(Per cent)			(Per cent)			(Per cent)			(Per cent)		
Grass												
Little bluestem	4.1	0.4	2.3	—	—	—	3.3	6.7	5.0	0.5	0	0.3
Blue grama	15.0	17.3	16.2	6.2	7.9	7.1	1.1	3.1	2.1	1.1	1.5	1.3
Parry oatgrass	.2	—	.1	—	—	—	.7	7.1	3.9	.1	1.6	.9
Arizona fescue	2.3	1.2	1.8	29.2	29.8	29.5	19.9	11.3	15.6	12.8	17.0	14.9
Mountain muhly	21.7	18.5	20.1	25.5	28.2	26.9	30.4	30.4	30.4	49.4	40.5	45.0
Other grasses	2.2	2.2	2.2	2.3	1.5	1.9	15.4	12.8	14.1	7.5	6.3	6.9
Sedge	5.4	4.8	5.1	3.7	6.3	5.0	4.6	1.8	3.2	4.0	7.5	5.8
Total grass and sedge	50.7	44.5	47.6	66.9	73.7	70.3	75.4	73.2	74.3	75.4	74.4	74.9
Weeds												
Rose pussytoes	18.1	26.6	22.4	7.6	5.4	6.5	6.8	10.4	8.6	4.4	3.3	3.9
Nickleaf milkvetch	2.2	.9	1.6	1.2	1.4	1.3	.7	.7	.7	1.9	2.7	2.3
Trailing fleabane	3.9	.6	2.3	.2	.6	.4	.3	1.6	1.0	.1	.9	.5
Fringed sagebrush	11.0	17.3	14.2	5.5	8.7	7.0	1.2	3.9	2.6	10.0	14.6	12.3
Other weeds	14.1	10.2	12.2	18.6	10.3	14.5	15.6	10.2	12.9	8.2	4.0	6.1
Total weeds	49.3	55.5	52.4	33.1	26.3	29.7	24.6	26.8	25.7	24.6	25.6	25.1
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

made up an average of 16 per cent of the total herbage. It was less abundant on moderately grazed areas and became a minor component on lightly grazed and ungrazed areas. Although it ocurred frequently, it did not become prominent except under heavy grazing use. Both Crafts (1937) and Nichol (1937) report similar trends for blue grama on overgrazed ranges in Arizona.

Little bluestem and Parry oatgrass were rarely prominent in the composition except on localized areas. Both species had a tendency to grow in colonies and were not uniformly scattered over the range. Consequently, there was no consistent frequency of their occurrence on the sample plots.

Other grasses, principally the wheatgrasses (*Agropyron* spp.), prairie junegrass (*Koeleria cristata*), and bottlebrush squirreltail (*Sitanion hystrix*) were not present in appreciable amounts except on light- and non-use areas. The wheatgrasses (principally *Agropyron smithii* and *A. subsecundum*) were more frequently associated with lighter rates of grazing, whereas tumblegrass (*Schedonnardus paniculatus*) and pullup muhly (*Muhlenbergia filiformis*) were more typical of the heavily grazed areas.

The weed cover on heavily grazed ranges formed more than half of the total composition, but was only about one-fourth of the total cover elsewhere. Rose pussytoes and trailing fleabane were prominent on heavily grazed areas and, in general, became consistently less prominent as grazing decreased. Fringed sagebrush was almost as abundant on none-use areas as on those heavily grazed, but was much reduced on both moderately and lightly grazed areas. Nickleaf milkvetch, a palatable legume, increased in frequency as the degree of grazing use was reduced, but was never an abundant part of the composition.

On pine-bunchgrass ranges in central Colorado, Arizona fescue and mountain muhly are the most important forage species in the herbaceous cover. Management, therefore, should be based on keeping these grasses in a healthy, productive condition. Little bluestem and Parry oatgrass may sometimes be abundant enough locally to provide substantial amounts of forage. An increasing abundance of blue grama (Fig. 2), rose pussytoes, trailing fleabane, and fringed sagebrush indicates that depletion is resulting from too heavy grazing use and that corrective measures are needed. On many ranges in the ponderosa pine zone, the native bunchgrasses have been completely eliminated and blue grama is the dominant grass species.

Occurrence

The number of plants per plot of most of the species was related to grazing intensity (Table II). Species reactions differ but the difference in response between the palatable and unpalatable species provides information for evaluating range-management practices.

Plants of blue grama was most abundant on heavily grazed plots and least abundant on lightly grazed plots. In contrast, plants of Arizona fescue, a palatable species, were more numerous on areas where utilization was moderate or less. Mountain muhly plants were most numerous on heavily grazed areas, but they were smaller and weaker plants. Actually, many of the units that appeared to be separate plants may have been the result of disintegration of originally larger clumps.

Plants of other species of grass were consider-

TABLE II. Average number of plants per plot in relation to grazing intensity, Manitou Experimental Forest—1949, 1950

Species	Past Grazing Treatment											
	Heavy			Moderate			Light			None		
	1949	1950	Ave.	1949	1950	Ave.	1949	1950	Ave.	1949	1950	Ave.
	(Number)			(Number)			(Number)			(Number)		
Grass												
Little bluestem	9.3	1.7	5.5	—	—	—	3.6	13.6	8.3	0.5	T*	0.2
Blue grama	27.7	32.5	30.1	26.3	21.7	24.0	4.6	7.2	5.9	7.8	7.9	7.8
Parry oatgrass	.8	0	.4	—	—	—	.9	9.6	5.2	.2	.9	.5
Arizona fescue	1.2	2.9	2.0	8.7	8.9	8.8	5.0	3.1	4.0	12.4	13.0	12.7
Mountain muhly	28.6	49.0	38.8	28.1	45.9	37.0	23.9	34.2	29.0	20.1	31.7	25.9
Sedge	110.9	102.6	106.7	47.4	70.4	58.9	59.0	29.1	44.0	38.6	69.0	53.8
Weeds												
Rose pussytoes	55.9	64.7	60.3	44.6	19.6	32.1	25.2	17.6	21.4	12.8	7.1	10.0
Nickleaf milkvetch	1.7	4.7	3.2	4.4	4.8	4.6	1.6	2.8	2.2	4.9	7.3	6.1
Trailing fleabane	30.5	10.9	20.7	4.6	17.4	11.0	7.1	22.1	14.6	4.4	9.7	7.0
Fringed sagebrush	18.5	20.5	19.5	11.5	12.7	12.1	6.1	4.3	5.2	15.4	14.2	14.8

*Less than 0.05 plant per plot

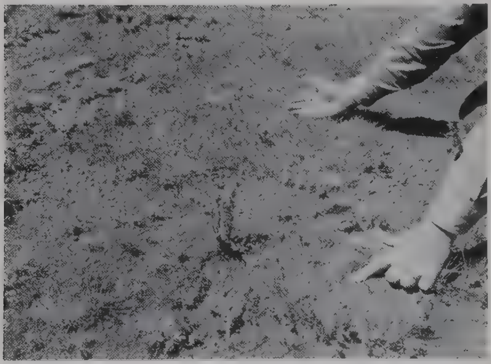

FIG. 2. Invasion of blue grama (upper) and deterioration of mountain muhly (lower) on heavily grazed pine-bunchgrass ranges.

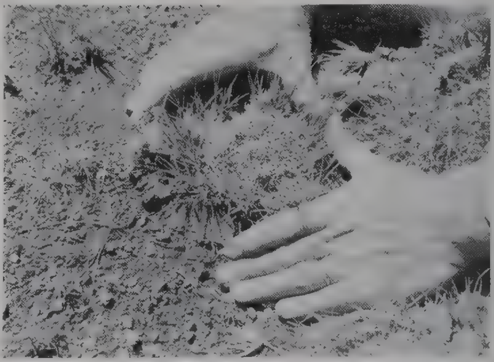

FIG. 3. Typical weak growth of mountain muhly on heavily grazed ranges. Small tufts of grass are confined to the perimeter of the crown.

ably more numerous on light- and non-use areas than on those grazed moderately or heavily. The number of sedge plants was not consistent between grazing intensities, but was greater on the heavy-use area.

The number of plants of rose pussytoes was greatest on heavy-use areas and least on ungrazed areas. Nickleaf milkvetch fluctuated too much to indicate any trend. Trailing fleabane was much more numerous on heavily grazed plots than on plots with other types of use. The number of plants of fringed sagebrush was less under lighter grazing, but was nearly as abundant on ungrazed areas as on those heavily grazed.

Growth habit

The growth form of the plants was also related to grazing intensity. The bunchgrasses had a greater number of grass tufts per plant on heavily grazed areas than on areas more conservatively grazed. The tufts, however, were small, weak growths, confined to the perimeter of the crown (Fig. 3). In many cases it was difficult to determine whether a group of plants had originally been a larger plant that had broken up into smaller units as a result of being weakened by too heavy use. On lightly grazed ranges, grass tufts were larger and scattered uniformly over the plant crown, and the crowns formed distinct units. Two types of dead centers of grass plants were conspicuous. Plants with dead centers resulting from old age still retained a comparatively wide band of vigorous growth around the edge of the crown, and stubble from previous years was abundant. Dead centers resulting from too heavy grazing were different. There was a noticeable lack of old growth on the plant, and the live parts of the crown produced a weak spindly type of growth.

Among the weeds, two species were conspicuous in the different growth forms associated with different intensities of grazing. Normal growth of nickleaf milkvetch is a spreading, semierect type of foliage, but on heavily grazed areas the leaves of the plants were prostrate. Fringed sagebrush, in competition with the native bunchgrasses on ungrazed areas, was an erect shrubby type of growth and produced numerous seedstalks. On grazed areas, particularly those moderately or heavily grazed, seedstalks were few but a dense basal growth, almost of mat form, developed.

Healthy condition in bunchgrass ranges is reflected in fewer plants of most species, but a more prolific and vigorous type of erect growth (Fig. 4). Ungrazed plants have a tendency to develop into large robust units. Extensive root systems are developed and invasion by other plants into bare soil areas is reduced to a minimum. Consequently, the lighter the degree of grazing use the greater is the tendency toward fewer but larger plants. Most species that occurred with sufficient frequency to establish clear-cut trends had a maximum number of individual plants on heavily grazed areas. Arizona fescue was an exception to this rule.

Seedlings

The number of grass seedlings on heavy-, moderate-, and light-use areas were about the same; 9.3, 9.6, and 8.0, respectively. On ungrazed areas, 15.9 seedlings per plot occurred. This indicates that the microclimatic conditions necessary for germination and growth of grass seedlings are more favorable under non-use than on grazed ranges.

Weed seedlings indicated a closer relationship to grazing treatment than the grasses. The number of seedlings of trailing fleabane and fringed sagebrush was greater on heavy-use areas than for the other areas. Seedlings of rose pussytoes were abundant on both moderate- and heavy-use areas. All of these species are commonly termed indicators of overgrazing. Nickleaf milkvetch seedlings were least abundant on the heavy-use areas and increased as grazing use became lighter. The number of weed seedlings per plot for the different past grazing intensities was as follows:

Species	Heavy	Moderate	Light	None
Rose pussytoes	3.8	6.1	1.1	0.2
Nickleaf milkvetch	1.1	2.1	3.7	11.1
Trailing fleabane	36.3	1.9	2.0	2.1
Fringed sagebrush	6.0	4.2	1.7	3.6

Seedstalks

Mountain muhly and little bluestem were the only two species that indicated a correlation between number of seedstalks per plant and the intensity of grazing use. Ungrazed plants of these species produced 10 to 12 times more seedstalks than plants heavily grazed. There was a noticeable lack of trend in all other species. Usually, Arizona fescue produces an abundance of seedstalks, but in 1949 they were very rare, even in the ungrazed exclosures. This indicates that other factors, such as weather, may be a controlling influence in seedstalk production.

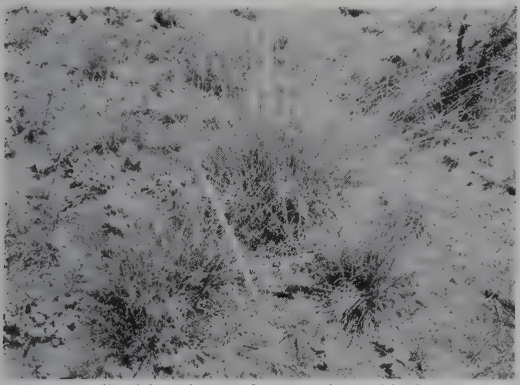

FIG. 4. Healthy plants of mountain muhly have a prolific and vigorous growth over most of the plant crown.

Height growth

One of the most consistent trends shown was the relationship between the height growth of the leaves of palatable plants and the intensity of past grazing use. In most cases, both the grasses and the sedges grew almost twice as tall under complete protection as they did on heavily grazed areas (Table III). These results indicate the reduced vigor of the plants is a result of heavy grazing pressure.

TABLE III. Average leaf height growth of major species, Manitou Experimental Forest—1949, 1950

Species	GRAZING TREATMENT							
	Heavy		Moderate		Light		None	
	1949	1950	1949	1950	1949	1950	1949	1950
	(inches)		(inches)		(inches)		(inches)	
Grass								
Little bluestem	3.0	1.8	—	—	3.8	2.9	2.4	3.0
Blue grama	1.7	1.1	1.8	1.3	2.3	1.5	3.0	2.0
Parry oatgrass	3.4	—	—	—	4.9	4.2	6.5	9.8
Arizona fescue	6.0	3.2	9.6	8.2	10.0	9.4	10.0	10.1
Mountain muhly	3.3	2.1	4.0	3.2	4.7	3.6	6.3	4.4
Sedge	2.9	2.4	4.1	3.2	4.2	2.8	5.8	4.2
Weeds								
Rose pussytoes	.5	.5	.5	.5	.5	.5	.7	.5
Nickleaf milkvetch	4.4	1.5	4.2	2.1	5.7	1.7	5.7	3.1
Trailing fleabane	1.0	.8	1.0	.7	1.0	.8	1.1	.5
Fringed sagebrush	2.5	1.9	2.9	2.3	2.5	2.4	4.1	3.5

The average leaf height of blue grama, Arizona fescue, and mountain muhly consistently increased from heavy use through moderate-, light-, and non-use. Even the sedges showed an increased height growth under lighter rates of grazing. This is one of the few factors studied in which the sedges showed a definite trend with respect to the intensity of grazing.

For the two unpalatable weeds, there appeared to be little or no relation between height growth and grazing use. Rose pussytoes and trailing fleabane made about the same growth on all areas. Nickleaf milkvetch showed differences similar to the palatable grasses. Height growth was least under heavy grazing and greatest on protected areas. Fringed sagebrush varied considerably, but height growth tended to be greater on the lighter use areas.

In using height growth as a measure of plant vigor, seasonal differences in growth cannot be ignored. In most cases, the height growth in 1950 was significantly shorter than in 1949 because of drought. Only 11.61 inches of precipitation fell during 1950, most of it in small amounts that had little effect on soil moisture.

Herbage yield

The total herbage clipped during 1949 from areas heavily grazed was 939 pounds per acre. In contrast, moderate-, light-, and non-use areas produced 1,175, 1,115, and 1,980 pounds per acre, respectively. An even greater contrast appeared in the yield of grass and sedge. Only 477 pounds per acre was produced on heavily grazed areas while 785, 841, and 1,493 pounds per acre were produced under moderate-, light-, and non-use, respectively (Table IV).

Yields in 1950 were much lower on all areas be-

TABLE IV. Yields of air-dry herbage by degrees of grazing use, Manitou Experimental Forest—1949, 1950

Species	GRAZING TREATMENT							
	Heavy		Moderate		Light		None	
	1949	1950	1949	1950	1949	1950	1949	1950
	(Pounds per acre)		(Pounds per acre)		(Pounds per acre)		(Pounds per acre)	
Grass								
Little bluestem	38	3	—	—	37	44	9	—
Blue grama	140	133	74	65	12	20	21	15
Parry oatgrass	2	—	—	—	8	46	2	15
Arizona fescue	22	9	343	247	222	74	254	165
Mountain muhly	204	143	299	233	339	199	979	392
Other grasses	20	17	26	13	172	84	149	61
Total	426	305	742	558	790	467	1414	648
Sedge	51	37	43	53	51	12	79	73
Total grass and sedge	477	342	785	611	841	479	1493	721
Weeds								
Rose pussytoes	170	204	88	44	76	68	89	32
Nickleaf milkvetch	21	7	14	11	8	5	37	26
Trailing fleabane	36	5	3	5	3	11	2	9
Other weeds	132	78	220	85	174	66	162	39
Total	359	294	325	145	261	150	290	106
Fringed sagebrush	103	133	65	72	13	26	197	142
Total	939	769	1175	828	1115	655	1980	969

cause of drought, but the differences related to grazing intensity followed the same general pattern. Grass and sedge herbage on heavily grazed areas in 1950 were reduced 28 per cent. On moderate-use areas the reduction amounted to 22 per cent; on light-use areas, 43 per cent; and on ungrazed areas, 51 per cent.

It is significant that in this comparison the moderately grazed areas suffered the least from drought and the non-use areas the most. Plants weakened by too heavy grazing would explain the greater damage on areas heavily grazed, but more study is needed to evaluate the proportionally greater decreases under light grazing and no use. Drought effects were reflected in reduction of top growth rather than in death of plants.

Herbage yield of individual species reflects the effect of different intensities of grazing. As an example, the yield of blue grama was highest under heavy grazing, but was very low under light- and non-use. This grass is relatively unpalatable on pine-bunchgrass ranges when bunchgrasses are available.

Arizona fescue and mountain muhly, the main forage grasses, produced an average of only 15 and 173 pounds per acre, respectively, under heavy grazing. Under moderate grazing, Arizona fescue produced an average of 295 pounds and mountain muhly, 266 pounds per acre. The yield of the latter was even greater under light grazing and under non-use, but Arizona fescue yields were less. Under light and moderate rates of grazing there is not enough use of fescue to weaken the plants and the variation shown is probably natural fluctuation in composition. Under heavy grazing, the cattle make heavier use of fescue, and since it is more susceptible to injury from heavy grazing, the yields are greatly reduced.

Little bluestem and Parry oatgrass were not plentiful enough to furnish reliable data on yields. The yield of other grasses, principally prairie junegrass, bottlebrush squirreltail, and several of the wheatgrasses, was highest under the lighter rates of grazing use. The yield of sedges did not appear to be related to grazing intensity even though the plants are palatable.

Among the weeds, rose pussytoes, trailing fleabane, and fringed sagebrush all produced higher herbage yields on areas heavily grazed than on those either lightly or moderately grazed. The production of fringed sagebrush, however, was heaviest on the ungrazed areas. Here a more favorable microclimate resulted in greater height growth and more seedstalks. Nickleaf milkvetch is a palatable plant, but in this study it produced greater yields under heavy and moderate grazing than under light use. Yields were maximum on non-use areas.

Root growth

Plants of little bluestem, Arizona fescue, and mountain muhly were dug from areas representative of each of the four grazing intensities studied. The air-dry weights of the roots in the surface cubic foot of soil were compared with air-dry weight of the tops to determine the ratio of the top growth to root growth (Table V).

TABLE V. Ratio of air-dry weights of top growth of major forage grasses to their root growth in the surface cubic foot of soil, Manitou Experimental Forest—1949

Species	GRAZING INTENSITY			
	Heavy	Moderate	Light	None
Little bluestem	2.37	3.86	3.32	3.69
Arizona fescue	2.53	3.20	3.10	3.22
Mountain muhly	2.71	3.63	3.35	4.20
Average	2.54	3.56	3.26	3.71

All three species indicated a similar response to grazing. On heavily grazed areas the plants produced about 2½ units of foliage to 1 unit of roots. On the areas grazed less heavily, the ratio for all species was about 3½ to 1 (Fig. 5). The variation among moderate-, light-, and non-use areas appeared to be normal differences but the ratio on the heavily grazed areas is a definite effect of grazing. This would indicate that moderate or lighter use of the plants by livestock does not weaken the root growth in the first foot of soil sufficiently to reduce their vigor.

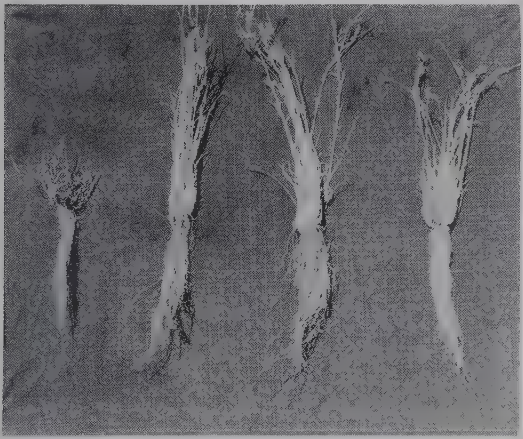

FIG. 5. Plants of little bluestem from (left to right) heavy-, moderate-, light-, and non-use areas. Root and top growth developments are typical.

Litter

The amount of herbaceous litter on the ground is important in determining the amount of precipitation that enters the soil (Johnson 1940). On heavily grazed areas, there was only 807 pounds of litter per acre compared with 1,174 pounds on the moderately grazed range; 1,115 pounds on the lightly grazed range; and 1,980 pounds on non-use areas. On the non-use areas, there was a definite humus layer beneath the litter. This was entirely absent on the heavily grazed areas. A humus layer was present on moderately and lightly grazed areas, but was not as pronounced as in the ungrazed enclosures.

Soil moisture

Soil samples were obtained from each of the exclosures at monthly intervals from June 15 to September 15 to determine what effect the different degrees of grazing had on soil moisture. The amount of soil moisture for June, July, and August was about the same on the heavy-, moderate-, and light-use areas at both the 0- to 6- and 6- to 12-inch depth (Table VI). On the ungrazed areas, however, moisture in the surface layer was about 43 per cent greater, and in the 6- to 12-inch layer about 48 per cent greater than on the grazed areas. Moisture content during June and July remained at about the same level, but dropped about 50 per cent during August and September.

TABLE VI. Soil moisture in relation to grazing intensity Manitou Experimental Forest—1949

Date	Soil depth	GRAZING INTENSITY			
		Heavy	Moderate	Light	None
	(Inches)	(Per cent)			
6/20/49....	0-6	14.02	12.96	13.18	19.10
	6-12	10.25	10.21	9.60	14.83
7/15/49....	0-6	14.56	14.65	13.00	20.20
	6-12	11.88	12.30	10.04	14.74
8/15/49....	0-6	7.22	8.85	7.49	9.60
	6-12	5.20	3.79	4.62	6.82
9/15/49....	0-6	6.41	7.59	9.38	12.61
	6-12	3.28	3.33	4.55	6.19

Rainfall during the week prior to the September measurements produced some interesting changes in the soil moisture conditions. On heavily and moderately grazed areas, soil moisture at both depths was less than in August but on lightly grazed areas surface moisture increased 2 per cent and on ungrazed areas it increased 3 per cent. The moisture in the 6- to 12-inch layer decreased similarly to that on heavy- and moderate-use areas. The increase in the surface soil moisture on light- and non-use areas is probably related to factors affecting infiltration such as litter, compaction through trampling, or others that are not yet thoroughly understood.

SUMMARY

A study was made to determine the effect of grazing intensity on plant composition, vigor, and growth of pine-bunchgrass ranges. Grassland parks in 6 pastures that had been grazed at 3 intensities by cattle, and ungrazed exclosures in each range unit furnished the background for the study. The dates when the desired intensities of grazing in the units were first achieved varied by units from 1942 to 1944. In 1949 and 1950, temporary exclosures in the grassland areas of the range units provided the seasonal response of the plants following the prescribed intensity of grazing. From these temporary exclosures and exclosures ungrazed since 1939, data were obtained on species composition and frequency, utilization, number of plants and growth habits, number of seedlings, seedstalk production, height growth, herbage yield, root development, and litter accumulation. The results of this study indicate the following conditions and responses may be expected on pine-bunchgrass ranges.

Grasses formed the bulk of the palatable forage used by cattle. Arizona fescue and mountain muhly were the most important and most abundant forage species.

Progressively increasing amounts of blue grama, rose pussytoes, trailing fleabane, and fringed sagebrush occurred on lightly, moderately, and heavily grazed range.

The ungrazed ranges were characterized by comparatively small numbers of large plants per given unit of area, although Arizona fescue occurred in markedly greater numbers on the ungrazed areas than under any other treatment. The grass tufts were large and uniformly distributed over the plant crowns. Heavily grazed areas were characterized by a larger number of smaller plants of some species with smaller grass tufts usually confined to the outside edge of the crown. Arizona fescue plants were both fewer in number and smaller in size on the heavily grazed area than under the other grazing intensities.

Grass seedlings were most abundant on ungrazed areas. There was no apparent difference in the density of grass seedlings on ranges grazed at heavy, moderate, or light intensities.

Weed seedlings were closely correlated with intensity of grazing. Rose pussytoes, trailing fleabane, and fringed sagebrush seedlings were most abundant on heavily grazed areas. Nickleaf milkvetch seedlings were most abundant on ungrazed areas.

The effect of grazing on production of seedstalks was obscured by adverse weather effects. Little bluestem and mountain muhly were the only species to show a correlation between seedstalk production and grazing intensity.

Height of leaf growth was the most consistent plant response to the different grazing intensities. Leaf growth was shortest on areas that had received heavy grazing and longer under the lighter grazing intensities. Variations in weather also have an effect on height of leaf growth, but differences between the different grazing intensities were consistent.

Root development in relation to top growth was impaired by heavy grazing use. No impairment of root growth was observed under moderate and light grazing.

Herbage yield of perennial grasses and sedges was greatest on ungrazed range and progressively less on the lightly, moderately, and heavily grazed ranges. Blue grama produced more on the heavily grazed range and least on the lightly and ungrazed ranges, whereas mountain muhly and Arizona fescue were least productive on the heavily grazed areas. Low valued weeds and fringed sagebrush tended to be most productive on heavily grazed ranges.

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CHANGES IN A CALIFORNIA ANNUAL PLANT COMMUNITY INDUCED BY MANIPULATION OF NATURAL MULCH[1]

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The dead plant materials above the soil surface in natural grasslands are usually referred to as litter, mulch, or plant residue. This material varies in position from lying directly on the soil to standing upright in a tangled mass. It may also be in all stages of decomposition and in many degrees of compactness. The kinds of plants which contribute to the mulch layer are many and therefore the nature of the material itself is varied.

For purposes of study and accurate description, the total mulch has been divided into layers. The upper portion of unconsolidated and undecomposed material is litter to the forester and the A_{00} layer in soil science. It has also been called fresh mulch and forage residue. The latter term seems the most descriptive for grasslands since much of that material may be eaten by livestock, however poor it is for feed. For example, the diet of animals grazing on the California annual type during the winter contains a considerable proportion of this material along with young and very succulent green herbage.

The partially decomposed material on the soil surface is known as raw humus, the A_0 layer or, preferably for grasslands, humic mulch. Little is ever easten by livestock. It becomes humus when decomposition proceeds to a point so that the origin of the material is no longer recognizable and it becomes mixed with mineral soil. Humic mulch is often missing if the total mulch layer is thin.

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[1] This paper is based on Project No. 1501 in the California Agricultural Experiment Station.

Mulch is used in this paper to include both layers and is a general term to be used when division into layers is unnecessary or impractical. The term "litter" should be restricted to its present usage in forestry.

These terms and definitions are in agreement with those used by Hedrick (1948) and only slightly different from suggestions made by Dyksterhuis and Schmutz (1947).

Sincere appreciation is expressed for the help in reading field plots and in making certain of the calculations that was given by Messrs. Harold Baker, James Mallory, Robert Merriam, and Lynn Rader.

LITERATURE REVIEW

The beneficial effects of mulches in farm crop production and in forest management have long been recognized. The manipulation and management of plant materials to protect the soil forms an important part of most soil conservation programs. The distribution, thickness, and occasionally the amount of mulch is often given importance in range management literature dealing with the appraisal and management of native grasslands. However, the foundation of quantitative data on which these statements have been made is not great and for grasslands it is scarce.

Dyksterhuis and Schmutz (1947) gave an excellent review of the literature which deals with mulches. Repetition of that review is hardly necessary but the reiteration of major findings seems pertinent. There is little doubt that a mulch layer improves soil surface conditions for plant growth and at the same time gives the soil protection against erosion. Less evaporation, less extremes in soil temperature, more organic matter in the top soil, more activity by organisms, and reduced impact of raindrops and running water are the main contributing factors. Infiltration is increased but at the same time mulch causes some water loss through interception. These may be summarized by saying that mulch improves soil structure and fertility and increases infiltration rate.

The effects on soil and water no doubt in turn influence the plants growing thereon. Increasing amounts of mulch have been shown to result in improved germination and emergence of grass seedlings (Glendening 1942). Forage production may be improved with increasing amounts of mulch (Larson and Whitman 1942, Schwan, Hodges, and Weaver 1949) but several authors have shown that accumulation of mulch could become excessive and thereby reduce forage production (Dyksterhuis and Schmutz 1947, Weaver and Rowland 1952). Any increase in mulch below optimum amounts has been said to promote plant succession but excessive amounts unquestionably smother some understory plants and reduce seed stalk formation of the dominant grasses (Weaver and Rowland 1952). A decrease in the proportion of grass and increased density in the California annual type were reported by Talbot, Biswell, and Hormay (1939) for two years following removal of mulch by hand. Hervey (1949) found similar results the first growing season after a fire.

Mulch accumulates as the above ground parts of plants die. The speed of decomposition depends upon microbial activity which require favorable combinations of temperature and moisture. These are seasonal phenomena in grasslands and result in a cycle of high and low amounts of mulch during a year (Dyksterhuis and Schmutz 1947). In addition the degree of forage removal by livestock, kinds of plants and the climate will also influence the deposition and decomposition of mulch. There is normally some carry-over of mulch from one year to the next. Hopkins (1954) in Kansas found that half the weight of materials placed on the ground was lost the first year and all had decomposed in three years.

Amount of mulch has been used as an important factor in the evaluation of range condition (Humphrey 1949). Voigt and Weaver (1951) give data from native pastures in Nebraska which show that the amount decreases with lowering condition and that changes in the composition of the mulch tend toward a high proportion of coarse materials in poor condition pastures.

These statements and studies suggest that maintenance of mulch is important in grassland management but many questions remain unanswered. What is the optimum amount which will promote maximum yearly and long-term production of forage? Is a complete cover of mulch needed at all times, is cover at certain seasons sufficient, or does only a certain proportion of the soil need to have a mulch? What are the effects of mulch on botanical composition? The following is a résumé of my experimentation to date on these questions.

LOCATION

The experiment was conducted on the Hopland Field Station which is operated by the University of California in Mendocino County. The location is in the central part of the North Coast ranges and receives an average annual rainfall of approximately 35 inches. The experimental plots were located on a relatively level area of Sutherlin soil that supports a typical stand of plants known widely as the California annual type. Perennial broadleaved herbaceous plants are scattered and occasionally individuals of purple needlegrass (*Stipa pulchra*) and other perennial grasses are found.

The study area was located near an area where winter feeding of sheep had been done for several years previous to 1952 when the work began. The range condition was poor, being principally an area of weeds and grasses with low forage value. The high potential production and low range condition were selected so that the influence of mulch manipulation on range improvement could be studied. The use pattern outside the fenced plots was changed in 1952 and by 1955 the condition of the surrounding area had improved markedly. These changes serve as useful comparisons with the experimental results.

METHODS

The experiment consisted of 64 adjacent plots each 10 feet on a side and arranged in an 8 x 8 latin square. The experimental area was enclosed by a sheep fence with a buffer strip 10 feet wide between the fence and plots. The lay-out was made in mid-winter of 1951-1952 so that a full crop of plants could be grown and measured before the first mulch treatments in August of 1952.

The outside plot corners were marked permanently with iron stakes so that all 64 could be located by stretching string in both directions across the experimental area. The 8 treatments, repeated each year on the same plots, were as follows:

1. Bare—all mulch removed and weighed.
2. Clipped to 1¼ inch stubble, clippings removed, weighed, none returned.
3. Same, 25 per cent returned.
4. Same, 50 per cent returned.
5. Same, 75 per cent returned.
6. Same, 100 per cent returned.
7. Clipped to 2½ inch stubble, clippings removed, weighed, none returned.
8. No clipping treatment or mulch removed.

Treatments 1-7 were clipped with a Scythette and the 1¼ inch stubble height is an average of the clipping height attained. The stubble and all mulch on Treatment 1 was removed by hand. The Scythette was held above the ground to attain the 2½ inch stubble height in Treatment 7. It, too, is an average measurement of height attained. Air-dry weights of the mulch were taken in the field at the time of clipping in the last week of August each year. In addition to these, the amount of mulch was sampled on one square foot of each of the 64 plots. The clippings from these were weighed after drying for 24 hours in an oven set at 100° C.

The treatments were applied in the last week of August from 1952-1955, which was at least 3 months after plant maturity and near the time when the first fall rain might occur. The time was chosen so that the least possible amount of seed would be removed with the mulch since most of it had fallen to the ground by that time. One objective was to determine the cumulative effects of mulch on botanical composition with as little disturbance of the seed crop as possible.

Sampling for forage production and botanical composition was done in late April or early May at a time near plant maturity. Sixty-four samples of one sqaure foot were clipped at ground level to determine current herbage growth on an oven-dry basis. Botanical composition was determined by the point system with 160 points used in each treatment. For each pin, all hits were recorded, the height of the first hit above the ground and whether the point hit bare soil, moss, mulch, or rocks at the soil surface.

CHARACTERISTICS OF THE FLORA AND VEGETATION

The flora within the exclosure used in the study is composed of at least 46 species. It is presented below in tabular form so that scientific and common names can be used separately and to give a general description of the vegetation. Even though the area described is small, the description of the vegetation typifies a much larger area. The scientific names of grasses are according to Hitchcock (1950) and all others follow Jepson (1925). The "I" and "N" in the third column refer to origin of the species in terms of introduced or native to California and is given on authority of Robbins (1940). Whether the species is annual or perennial is indicated by the "A" or "P" in the last column (Jepson 1925).

GRASSES

Aira caryophyllea—Silver hairgrass	I	A
Aristida oligantha—Prairie threeawn	N	A
Avena barbata—Slender wild oat	I	A
Briza minor—Little rattlesnake grass	I	A
Bromus mollis—Soft chess	I	A
Bromus rigidus—Ripgut	I	A
Festuca dertonensis—Foxtail fescue	I	A
Gastridium ventricosum—Nitgrass	I	A
Stipa pulchra—Purple needlegrass	N	P

LEGUMES

Astragalus nigrescens—Annual loco-weed	N	A
Lotus micranthus—Dwarf lotus	N	A
Lupinus bicolor—Annual lupine	N	A

Medicago hispida—Bur clover I A
Trifolium bifidum—Pinole clover N A
Trifolium ciliolatum—Tree clover N A
Trifolium depauperatum—Dwarf sack clover N A
Trifolium microcephalum—Small headed clover N A
Trifolium microdon—Valparaiso clover N A
Trifolium variegatum—White tip clover N A

OTHER BROADLEAVED HERBS

Achyrachaena mollis—Blow wives N A
Agoseris heterophylla—Variable-leaved dandelion N A
Anagallis arvensis—Scarlet pimpernel I A
Baeria chrysostoma—Goldfields N A
Brodiaea capitata—Blue dicks N P
Calochortus venustus—White mariposa lily N P
Cerastium viscosum—Mouse-ear chickweed I A
Daucus pusillus—Rattlesnake weed N A
Eremocarpus setigerus—Turkey mullein N A
Erodium botrys—Broadleaf filaree I A
Filago gallica—Filago I A
Galium californicum—California bedstraw N P
Galium parisiense—Wall bedstraw I A
Hypochoeris glabra—Smooth cat's ear I A
Lepidium nitidum—Shining peppergrass N A
Linanthus ciliatus—Whisker-brush N A
Micropus californicus—California micropus N A
Microseris acuminata—Pointed leaved microseris N A
Oenothera ovata—Sun cup N P
Orthocarpus densiflorus—Owl's clover N A
Orthocarpus erianthus—Johnny tuck N A
Orthocarpus pusillus—Dwarf's owl's clover N A
Pentachaeta exilis—Small pentachaeta N A
Plagiobothrys nothofulvus—Popcorn flower N A
Plantago erecta—Annual plantain I A
Sanicula bipinnatifida—Purple pincushion N P
Silene gallica—Common catchfly I A

TABLE I. Comparison of percentage botanical composition between years and types of plants

	1952	1953	1954	1955
Annual	99	98	99	97
Perennial	1	2	1	3
Introduced	89	92	97	80
Native	11	8	3	20
Grasses	43	48	59	29
Legumes	9	6	3	17
Other herbs	48	46	38	54

The vegetation within the exclosure contained a high proportion of annual plants (Table I). On the basis of percentage composition, the annuals contributed between 97 and 99 per cent of the foliage cover during the four years. The perennials were species of *Stipa, Brodiaea, Calochortus, Galium, Oenothera,* and *Sanicula.* These constitute 13 per cent of the 46 species in the flora but only 1 to 3 per cent of the cover.

When the breakdown is on a basis of whether the species are native or introduced, a somewhat different picture is presented. The composition contribtued by introduced species was between 80 and 97 per cent. The 16 alien plants make up 35 per cent of the floral list. Of these *Aira, Briza, Bromus mollis, Erodium, Festuca,* and *Hypochoeris* contributed all but a few per cent of the alien portion. They were at the same time the most important species in the whole vegetation in the study area. During the four years, they did not fail to make up at least 67 per cent of the entire botanical composition and in 1954 they comprised 84 per cent. Four others, *Avena, Gastridium, Bromus rigidus,* and *Medicago,* were present in very small amounts, even though they were abundant nearby and are commonly listed as important components of the California annual type. The principal natives were *Stipa,* all legumes, *Baeria, Pentachaeta, Linanthus, Daucus, Orthocarpus,* and *Lepidium.*

The present vegetation is clearly dominated by introduced annuals. The nature of the original grassland in California is little known and much controversy exists over the relative importance of native perennials and annuals and introduced annuals. Undoubtedly, the advent of alien plants, grazing by domestic animals, and change in the pattern of burning have resulted in a different vegetation than that of a century or two ago. A discussion of these points is not intended here but it does seem pertinent to record an observed change near and within the exclosure used for the experiment.

When the area was selected in late 1951, not a single plant of *Stipa pulchra,* a perennial bunchgrass, was noticed either in the exclosure or in the immediate vicinity. This was also true during the sampling at the end of the 1952 growing season. In late April of 1953, there were 193 small plants of *Stipa pulchra* within the exclosure and a scattering of them in the adjacent area. The number was 220 in 1954, and 612 in 1955 at which time there were large mature plants and many seedlings. A similar increase was apparent outside the exclosure but grazing prevented the formation of large bunches. *Stipa* plants were found in many of the mulch plots but no relationship to the treatments could be detected. The spread of this plant is continuing but how thick the stand will become and whether other perennial grasses will appear are still points of speculation.

The general appearance of the vegetation is that of grass even though the proportion of grass species has been only between 29 and 59 per cent. These plants are tall and remain standing during the dry season. The legumes are short and form an understory which is never obvious except upon close examination. The broadleaved herbs shatter and largely disappear shortly after they mature.

In some years and locations, *Lupinus bicolor* gave a brilliant blue aspect for a short period when it was in flower. *Erodium botrys* was neither tall nor did it have conspicuous flowers and even though it was abundant, the contrast in appearance was only on shade of green. In areas where grass was scarce, and in early spring when the grass was short, there were often patches of brilliantly colored flowers. The two most common of these were first the light yellow of *Orthocarpus erianthus* and later the orange-yellow of *Baeria chrysostoma*. Mixed with them were white splashes of *Calochortus venustus, Daucus pusillus, Plagiobothrys nothofulvus,* and others. In addition to the lupine, scattered spots of *Brodiaea, Trifoliums, Orthocarpus,* and *Sanicula* added bits of blue and red to the aspect.

Amounts of Mulch

The average amount of mulch on an acre basis which was attained per treatment is shown in Table II and illustrated in Figure 1. Two trends are at once apparent. There has been a gradual increase in mulch for Treatments 2-8 from 1952 to 1955. The treatments with greatest proportion of current herbage growth returned to the plots have shown the greatest percentage increase in mulch over the 4 years.

Table II. Average pounds of mulch per acre on the eight treatments after manipulations in the last week of August each year

Treatments	1952	1953	1954	1955
1	0	0	0	0
2	945	1175	1310	2410
3	1080	1450	1510	2690
4	1210	1820	1960	3115
5	1310	2060	2000	3375
6	1540	2440	2475	4065
7	1100	1870	2065	4145
8	1485	2360	3220	4990

An explanation for both trends is found in the nature of the treatments themselves. Only current growth was used in the manipulation while the mulch measurements included current growth and undecomposed residue from previous years. The carry-over was apparent, especially from 1954 to 1955, and was shown by percentage of the soil surface covered (Table III) and by field observations as well as in the data mentioned above.

General differences between years in the rate of decomposition and the influence of amount of

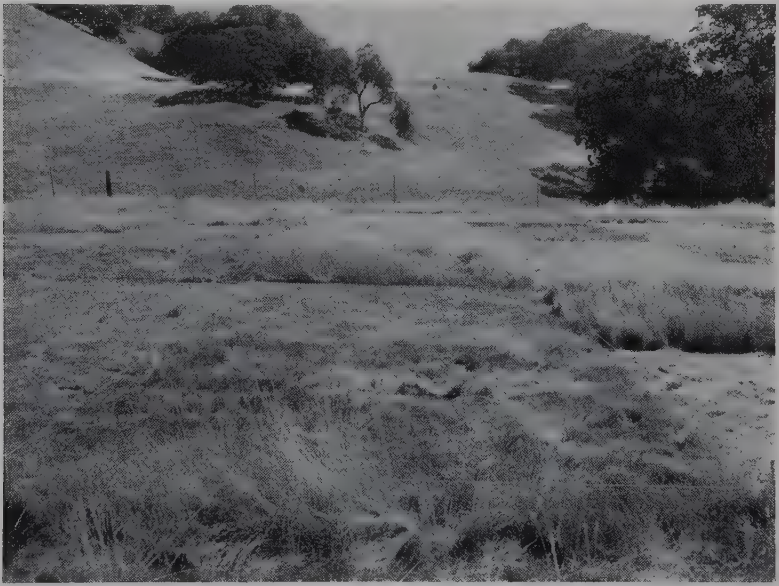

Fig. 1. Different amounts and position of mulch September 15, 1954. Stubble height on the plot in the foreground was 2.5 inches, on the second 1.25 inches and the third plot was unclipped.

Table III. Percentage of the soil surface covered by mulch and moss in the various treatment from 1952 to 1955

Treatment	Mulch					Moss				
	4-4-52	4-29-53	11-4-53	4-26-54	4-26-55	4-4-52	4-29-53	11-4-53	4-26-54	4-26-55
1....	20	0	19	39	25	56	27	0	17	37
2....	15	0	79	71	70	61	23	4	4	21
3....	21	1	82	68	86	53	20	2	4	13
4....	20	1	92	74	84	68	21	0	2	11
5....	15	4	94	73	87	66	19	0	2	10
6....	22	1	97	79	97	60	25	0	2	3
7....	21	0	80	78	85	58	30	0	2	13
8....	22	1	92	80	83	40	20	0	4	8

mulch on decomposition are shown. The full extent of these differences and trends needs to be studied further before the complete cycle of deposition and decomposition can be told.

Soil Surface Conditions

In the sampling with the point system, a record was made of whether the points hit mulch, bare soil, moss, or rocks at the soil surface. Rocks will not be mentioned further because that item included only about a quarter of one per cent of the hits.

The proportion of hits on mulch, bare soil, and moss varied greatly between years with very little difference between treatments except that the bare treatment had considerably less mulch and more bare soil and moss than the others in 1954 and 1955 (Table III).

The data for 1952 were taken before any mulch manipulations were made and they reflect the conditions at the beginning of the experiment. Roughly one-fifth of the soil was bare, one-fifth covered with mulch, and three-fifths covered with moss. At the same time of year in 1953 and after one set of treatments, there was practically no mulch on any plots, only about 23 per cent was moss and the remaining soil between the growing plants was bare. The mulch could have been lost only through decomposition. The winter of 1952-1953 was relatively moist and warm, conditions favorable to rapid decomposition. At the same time, there was practically no accumulation of mulch older than that left in August of 1952. Carry-over of mulch began in this experiment with the winter of 1953-1954.

In the following two years, the percentage of the soil covered with mulch was high except for Treatment 1. The 39 and 25 per cent found there, respectively, in the two years were higher than expected because an attempt was made to remove all of the mulch each year. However, close examination showed that a layer of fine materials still remained after treatment and also, by sampling time each year some plants had lost leaves and a few had matured and scattered. The extent and pattern of this addition to the mulch was not determined.

Between November, 1953, and April, 1954, there was an expected decrease in proportion of soil covered with mulch which ranged from 2 to 21 per cent. Just why it increased at the same time for the bare plots is not known. The average temperatures were lower in 1954-1955 than in other years and consequently the extent of the mulch covering was higher in the spring of 1955 than in the other years. The first two treatments did not follow this trend; again, the reason is unknown.

Evidently moss responded to differences in yearly environmental conditions just as the seed plants did. There was relatively little in 1954 and more in 1953 and 1955. By 1955, an inverse trend with amounts of mulch was developing.

Treatments 6 and 8 deserve special mention. Both had the maximum amount of mulch. The difference was that in Treatment 6 the plots were clipped to a stubble height of 1.25 inches and all the material was returned evenly to the plots. The soil in this treatment had a high coverage of mulch. In Treatment 8, the mulch was more upright and less of the soil was covered. This difference in position of the mulch contributed to the differences in speed of growth, botanical composition, and herbage production on these plots.

Production of Herbage

The oven-dry production of plant materials varied somewhat from year to year. In 1952, the amount was low on all treatments and not significantly different between plots. Thus, the experiment began with essentially uniform conditions of low forage production. Production was higher in 1953 on all treatments, still higher in 1954 and somewhat lower in 1955 than in 1954.

The most striking feature was the difference between treatments. Where all the mulch was removed, changes in production in 4 years were not significant and in 1955 this treatment still had a uniformly low yield. Production had not improved even though there had been no disturbance of the vegetation during the growing season.

With increasing amounts of mulch in the other treatments, the production increased. The dependence of production on mulch is shown in Figure 2 by the regression line which is expressed by the equation $Y = 1214 + 0.354X$. This means that for each pound of increase of mulch there was an increase of 0.354 pound in production between the limits of 1,200 and 2,400 pounds. These data have a highly significant correlation coefficient of 0.727. Figure 2 is based on the data obtained in 1954 and 1955 only. The first two years were omitted because the effects of mulch were still accumulating.

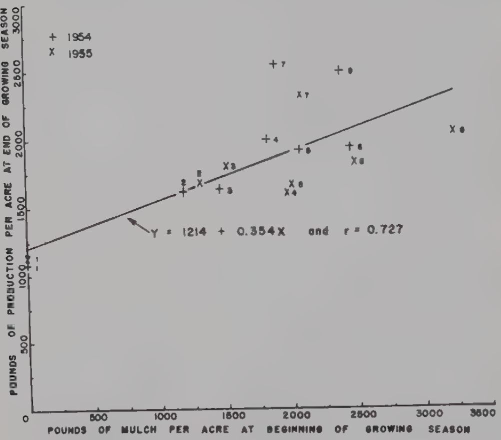

FIG. 2. Linear regression of pounds of production per acre on pounds of mulch for eight treatments in 1954 and 1955. Above 1214 pounds of production there is an average increase of 0.354 pounds of production for each additional pound of mulch. The correlation coefficient of 0.727 is significant at the 0.01 level.

When Treatments 7 and 8 are omitted, the relationship becomes much closer, as expressed by a correlation coefficient of 0.891. These perhaps should be omitted because they involved different stubble heights and therefore they include the factor of position of the mulch as well as the amount. However, the regression equation is little different when they are excluded except that the *beta* coefficient as a much narrower range of variation.

At this point, a discussion of the predictive value of the chart should be made. The experiment included the removal of all current growth each year as well as the removal of none. Neither of these conditions is practical in a grazing program aimed at maximum livestock production for the long-run. Somewhere between the two extremes should be a point of maximum sustained production. The proposal of a single point is not logical from these data alone because the relationship is linear and without a breaking point of production indicated. Other factors must be considered such as botanical composition, speed of growth, length of growing season, soil stability and, above all, the animal requirements and over-all ranch operation before a level of proper use can be indicated.

The herbage production data are from samples clipped at ground level. The amount of mulch needed to allow a certain production can be read from the graph. For example, 2,000 pounds of mulch per acre are needed to obtain about 1,800 pounds of production. At first glance, this would indicate that none of the forage could be harvested because production is less than the mulch. However, some can be harvested because a portion of the mulch is carry-over from previous years. The amount of carry-over is greater with materials standing upright than with those flat on the soil surface. Since the amount of plant materials that decomposed completely each year varied a great deal and was not satisfactorily determined, Figure 2 cannot be used to determine the amount of forage that can be harvested by livestock. Production alone should not be the sole consideration in determination of proper use because proper kinds of plants and quality of forage are also needed for profitable livestock production. In short, these data show the dependency of herbage production on amounts of mulch but they do not differentiate between current additions to the mulch and carry-over. This must be done before interpretations of proper use by livestock can be made.

VEGETATIONAL DIFFERENCES BETWEEN TREATMENTS

Differences in botanical composition between treatments were not significant at the end of the first growing season in 1952. *Bromis mollis* made up 2.3 per cent of the composition, other grasses 40.6 per cent, *Erodium botrys* 15.4 per cent, all legumes 9.4 per cent, and all other broadleaved plants 32.3 per cent (Table IV). Analysis of variance after angular transformation showed no significant differences between the treatments within any of these groups. Thus, the initial objective of essentially uniform composition between the mulch treatments was accomplished. There were some location effects as indicated by significant differences in the rows and columns. These were expected and were the principal reasons for using the latin square design. By so doing, the variance due to location could be separated from the variance due to treatment.

Several trends in composition became apparent in successive years. Some were striking by 1953 and others developed more slowly. Several species responded very definitely to the mulch treatments while others did not. Some were favored when all the mulch was removed, others when none was removed and a third group reached a

TABLE IV. Percentage botanical composition for treatments and years. Each percentage is an average of eight replications in a latin square design

	Year	TREATMENTS								Average
		1	2	3	4	5	6	7	8	
Bromus mollis....	1952	0.9	2.0	2.6	2.3	6.5	0.8	1.8	2.7	2.3
	1953	4.4	12.9	11.4	14.6	14.3	12.7	7.0	14.5	11.5
	1954	1.9	11.0	5.5	16.1	12.4	12.4	16.4	37.3	14.1
	1955	0.9	6.0	7.0	7.4	7.4	12.9	16.8	25.8	10.5
Other grasses....	1952	43.6	50.2	44.1	39.2	31.5	36.5	42.3	36.4	40.6
	1953	39.9	34.3	40.9	27.2	29.6	34.8	47.1	36.6	36.3
	1954	47.4	45.9	52.8	39.9	45.3	40.3	54.6	31.3	44.7
	1955	34.0	30.0	16.0	18.1	12.5	12.0	13.9	11.0	18.4
Legumes........	1952	6.8	11.1	11.0	10.8	7.6	7.1	8.1	12.7	9.4
	1953	5.4	7.9	6.0	6.3	10.6	6.3	0.6	5.2	6.1
	1954	2.8	5.9	4.2	1.6	1.5	2.1	0.9	1.5	2.6
	1955	4.5	20.8	24.2	19.4	21.3	17.7	17.9	8.2	16.8
Erodium botrys...	1952	14.5	17.2	7.6	13.8	17.4	15.9	15.3	22.7	15.4
	1953	15.3	20.2	12.8	23.8	19.1	16.3	17.8	34.3	20.1
	1954	22.3	21.2	18.3	18.1	16.3	19.7	16.7	17.0	18.7
	1955	35.0	29.3	25.5	36.9	36.1	36.3	38.7	40.0	34.7
Other broad-leaved plants....	1952	34.2	19.2	34.7	33.9	37.0	39.7	32.5	25.5	32.3
	1953	34.5	24.7	29.5	28.2	26.5	29.8	25.6	9.3	26.0
	1954	25.6	16.1	19.2	24.2	24.4	25.3	11.3	12.9	19.9
	1955	25.6	13.9	27.3	18.2	22.7	21.0	12.7	15.0	19.6

maximum composition with intermediate mulch treatments (Figure 3).

Grasses

Bromus mollis reached its highest proportion with the most mulch and was least with no mulch. It showed a definite gradation in the intermediate treatments although there was no significant difference in the proportion in Treatments 4 to 7. These changes did not become obvious until after two years of mulch treatment.

The response of *Aira caryophyllea* was the reverse of that shown by *Bromus mollis*. Large amounts were present with no mulch while the least occurred where there was maximum mulch. Only slight tendency toward this trend appeared in 1953. By 1954 it was definitely shown between the two extremes of treatment. In 1955, the percentage was very much higher where mulch was absent than on the other treatments and at the same time it was low on the 4 treatments with the most mulch.

All the other grasses including *Festuca dertonensis, Briza minor, Gastridium ventricosum, Bromus rigidus,* and a few others did not show significant differences due to mulch treatment. However, by 1955, they too seemed to be following the trend described for *Aira caryophyllea*. Perhaps they will respond with treatment in additional years. Aside from *Festuca dertonensis,* they made up a small proportion of the stand.

Legumes

The legumes as a group did not contribute over 17 per cent of the composition in any year and in 1954 they were under 3 per cent. Consequently, the sample was small and trends due to mulch treatments were over-shadowed by yearly differences. However, the extremes in mulch treatments seemed to result in low percetnages while small amounts of mulch allowed the greatest development of legumes. *Trifolium ciliolatum* and *Lupinus bicolor* each made up about one-third of the composition and 8 other species contributed the additional one-third.

Erodium botrys

Treatment differences were significant at the 5 per cent level. However, only two treatments were different from the others. An intermediate mulch treatment was low in all years and the most mulch gave the highest percentage of *Erodium*. When the composition percentages for 1955 were adjusted by regression to a constant percentage for 1952, no significant differences were found between treatments. Those treatments which had large amounts of *Erodium* in 1952 also were high in 1955. Thus, treatment of mulch in the manner of this experiment had little effect on the percentage of *Erodium* in the composition.

Other broadleaved species

Baeria chrysophylla responded quickly and markedly to the mulch treatment. By the end of

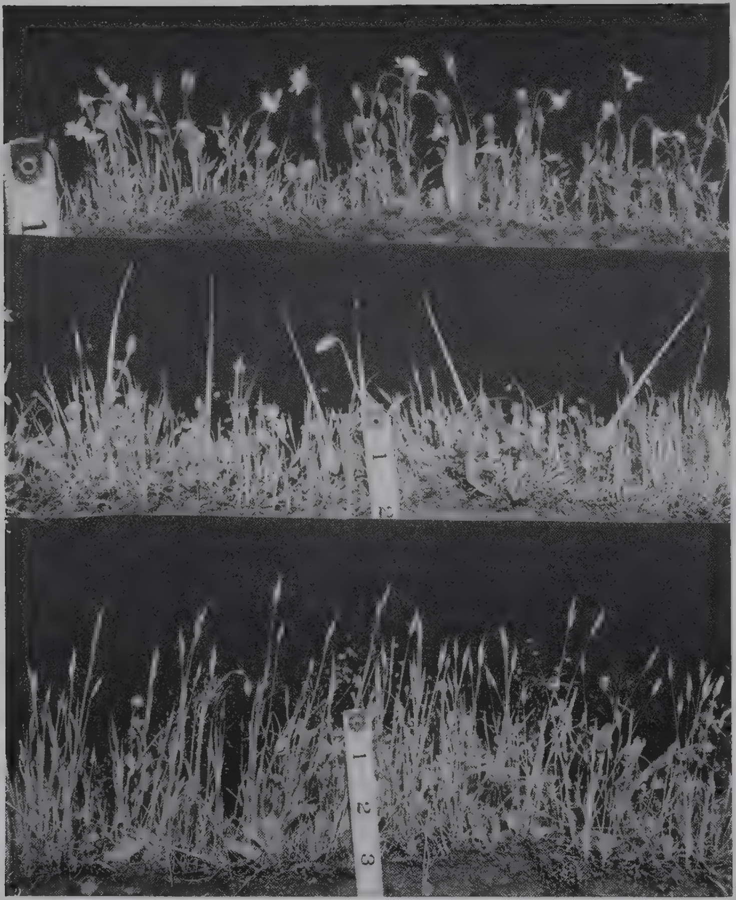

Fig. 3. These three one-inch thick strips of vegetation illustrate some of the differences in percentage botanical composition and height found with manipulation of mulch. The upper occurred only where all mulch had been removed. *Baeria chrysostoma*, *Pentachaeta exilis* and *Aira caryophyllea* were the abundant plants. The middle strip also shows short growth but a composition of small grasses, legumes and *Erodium botrys*. The tallest growth and importance of *Bromus mollis* where the greatest amounts of mulch occurred are illustrated in the lower strip.

the growing season following the first mulch treatments, this plant showed highly significant differences from a large percentage in the bare treatment to a low percentage with greatest mulch. The trend between the two extremes was obvious on the ground as well as in the data. When the golden-colored flowers were open, the plot boundaries and treatments were conspicuous by varying amounts of the plants. *Hypochoeris glabra, Linanthus ciliatus, Pentachaeta exilis, Orthocarpus erianthus,* and *Galium parisiense* exhibited much the same tendencies as *Baeria* although to a lesser degree.

When all of the broadleaved plants except legumes and *Erodium* were considered as a group, it was found that increasing amounts of mulch resulted in a decreasing proportion of broadleaved plants.

In summary of the effect of mulch on botanical composition, several points need to be made. *Erodium* was found not to show a significant relationship between the percentages at the beginning and end. It would seem that amounts of it had little relationship to the mulch treatments. Two plants, *Bromus mollis* and *Baeria chrysostoma* were very sensitive to the treatments. *Aira caryophyllea* and *Hypochaeris glabra* were indicative also but not as sensitive as the first two.

The data indicate that mulch has a direct effect on composition. It may also have an indirect effect through competition. For example, plants of *Bromus mollis* were in greatest numbers with most mulch and *Baeria chrysostoma* was least. *Baeria* might have responded differently if the *Bromus* had been absent.

VEGETATIONAL DIFFERENCES BETWEEN YEARS

The effects of the yearly march of weather on vegetation has been widely recognized. It is very striking in the California annual type and most field studies must recognize this variable. Starting from seed each fall, as they do, makes these annuals very responsive to differences in environmental conditions. They must be able to germinate, grow, and produce seed each year. Since no two species respond alike, there is little wonder that the vegetation takes on different appearances from one year to the next. Table IV shows some of these differences but it must be recognized that effects of mulch are cumulative so that the data must be interpreted accordingly.

One of the most striking changes was the large proportion of *Erodium botrys* in 1955 (Figure 4). This plant has a large seed, germinates quickly when moisture arrives, and develops a long tap root in a few days. Something over an inch of rain in the last of August, 1954, fostered germination at that time. Even though the next rain did not come until October 15, many *Erodium* plants survived. With the advent of the later rains, another crop of seedlings appeared. For several months during the winter two age groups of *Erodium* were present. The winter of 1954-1955 was an especially cold one, total rainfall was light, and there was a long period in early spring without rain. The period of flush growth came in late April and early May and was a short one. Whatever the causes, *Erodium* produced an exceptionally large amount of herbage. It contributed much more to the percentage composition than in any previous year irrespective of mulch treatment.

The small annual legumes did not germinate with the August rain in 1954. However, by the end of the growing season these plants were much more evident than in previous years. In general terms, 1955 was a good year for clover and 1954 was a poor year. Differences among the legume species were not evident. All were either abundant or rare in the different years.

On a percentage basis, when some components of the vegetation increases others must decrease. There were fewer grasses in 1955 even though they were abundant in 1954 (Figure 5). Other types of broadleaved plants were about the same in 1954 and 1955 and in both years less than in 1952 and 1953. The small percentage of *Bromus mollis* in 1952 is probably a result of heavy grazing before the experiment began.

In general terms, 1955 was a good year for *Erodium* and legumes and a poor one for grass. Grass did relatively better from 1952 to 1954 and 1952 could be considered a fair clover year.

Analysis of variance after angular transformation of the percentages showed highly significant yearly differences within the 5 categories in Table IV and for *Aira carophyllea, Festuca dertonensis, Baeria chrysostoma, Hypochoeris glabra,* and *Linanthus ciliatus*. The F ratios ranged between 8.20 and 35.28. Variance was not calculated for other species because they were too scarce for the samples to be adequate.

RATE OF PLANT DEVELOPMENT

Ordinarily in the California annual type, germination begins immediately following the first fall rain of about half an inch. Precipitation fell nearly every day between October 10 and 19, 1953, for a total of 1.73 inches in the period. By November 4, the heights attained by the new plants were very obviously different on the various mulch treatments. *Bromus mollis* was found to average 0.81 inch in height where there was no mulch and 2.98 inches on the treatment with the most mulch. The heights on intermediate mulch treatments were between these two extremes. The correlation coefficient between the weight of mulch on August 27, 1953, and the heights of *Bromus mollis* was 0.718 which is significant at the .05 level. It indicates a positive relationship between amounts of mulch and plant development.

The observed differences in heights of *Bromus mollis* on November 3, 1953, seemed to be closely related to the height of stubble or position of the mulch. A highly significant correlation coefficient of 0.943 was found between the heights and stubble of *Bromus mollis*. Thus, position of the mulch is an important factor as well as the amount.

HEIGHT OF VEGETATION

The height of plant materials above the ground was ascertained by measuring the distance between the first hit of the pins and the soil surface. This is not a measurement of maximum height of plants but an attempt to obtain a height of vegetation. If the vegetation is tall or short, this type of measure should indicate the differences. One advantage of the sample is that it is objective and relatively free from personal bias. Another is that the understory plants are included

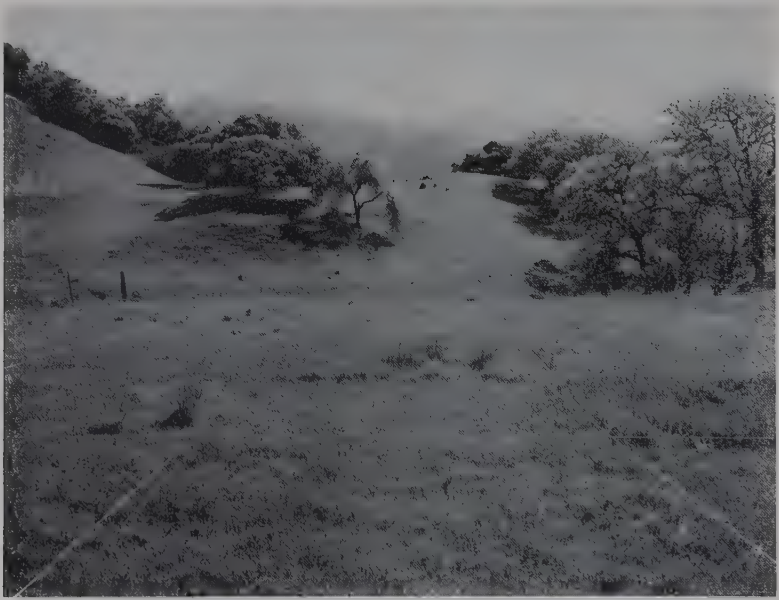

Fig. 4. On April 26, 1955, the proportion of grass to broadleaved herbs was low on all plots and the vegetation was shorter than in other years. *Erodium botrys* was the highest of any species in percentage composition. The large bunches are *Stipa pulchra.*

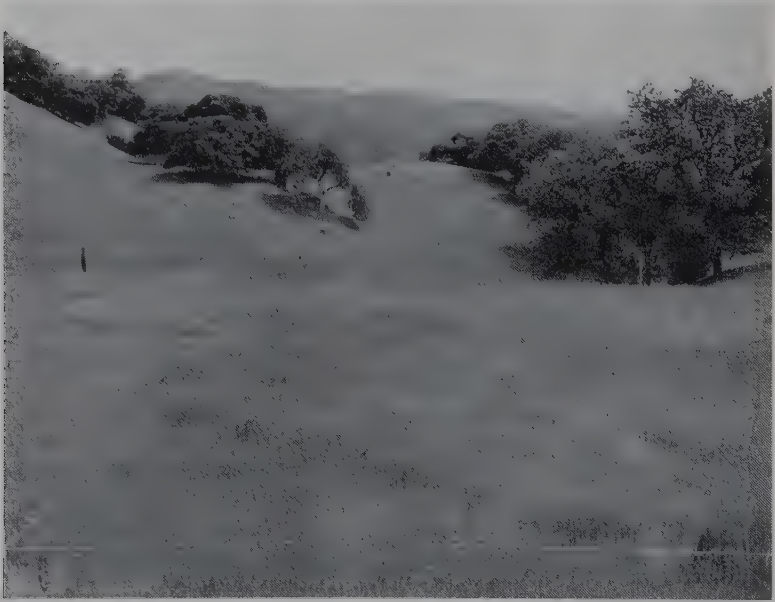

Fig. 5. On April 27, 1954, the proportion of grass to broadleaved herbs was high on all plots. The vegetation was taller than in other years of the study.

in the determinations. The measurements are on the same plants that are tallied as hits to compute botanical composition. Height of plant materials is a characteristic of vegetation and measurements of height should have intrinsic value.

The averages of all heights by treatment are shown in Table V. Considerable and significant differences occurred between years. In 1954, the grasses grew very well and their height is reflected in the average for that year. *Erodium botrys,* a plant of low stature, was relatively more important in 1955, a fact indicated by the low average height.

TABLE V. Average heights in inches of vegetation by treatments and years

Treatment	4-29-53	4-26-54	4-26-55
1	2.84	3.29	1.14
2	3.08	4.10	1.68
3	3.15	3.78	1.71
4	3.12	3.95	1.59
5	2.95	3.90	1.88
6	3.12	4.21	1.58
7	2.97	4.56	1.97
8	3.55	5.90	2.33
Average	3.10	4.21	1.74

Treatment differences within 1954 and 1955 were highly significant. In all three years, the treatment without mulch had the lowest vegetation while the tallest vegetation was where the most mulch occurred. Variations among Treatment 2-7 generally were not significant. Observations during the growing season led to a general conclusion that the height of plants at any time was at least in part dependent upon the height and position of the mulch. The fact that stubble heights were 0 for Treatment 1, 1.25 inches for Treatments 2-6, 2.5 inches for Treatment 7, and about 6 inches in Treatment 8 would indicate a positive relationship with the heights shown in Table V. Position and height of mulch has a direct influence on growth of plants as well as on yield and ground coverage.

GROUND COVER

Ground cover or coverage is here defined as the percentage of the soil surface covered by living plants. It has been referred to frequently in range management work as density. The concept is an important one and is commonly used in the description of vegetation. Coverage data were obtained by the point system as simply the percentage of pins which hit living plants.

In this experiment coverage proved to be a very insensitive measure of the effects of mulch (Table VI). Location differences within years were quite pronounced and were indicated by highly significant row and column effects. The variance within treatments was also significant but the between treatment differences were not. Yearly differences in coverage were of the greatest magnitude and highly significant. It would appear that differences in coverage in the kind of vegetation used in this experiment were related more to location within any one year and to compositional differences between years than to compositional differences which resulted from the different treatments. If this can be extended to the entire California annual type, then coverage or density as such becomes of little value as a guide to range condition and for evaluating grazing practices. On the other hand, the coverage by species can be used to compute percentage botanical composition quite effectively.

TABLE VI. Percentage of the soil surface covered by living plants

Treatment	1952	1953	1954	1955	Average
1	82.5	69.4	79.4	50.0	70.3
2	76.2	67.5	85.6	63.1	73.1
3	85.0	59.4	83.8	61.3	72.4
4	87.5	70.6	81.9	65.6	76.4
5	72.5	68.7	89.4	57.5	72.0
6	82.5	73.7	81.3	59.4	74.2
7	82.5	62.5	86.3	68.1	74.6
8	85.0	66.9	73.8	61.3	71.8
Average	81.7	67.2	82.7	60.8	

DAMAGE BY FROST

Damage to seedling plants by frost heaving is often observed in California (Biswell, *et al.* 1953). Several times each winter, the various treatments were examined for this type of damage. In no case was frost heaving observed where the soil had a cover of mulch. On the other hand, heaving was observed on several occasions where there was no mulch. Legumes especially and occasionally individuals of the other species, except *Erodium botrys,* were found on the bare plots that had been heaved by frost. This factor undoubtedly contributed to the changes in composition on the bare plots as well as the lack of mulch.

EROSION AND RUNOFF

The plots were examined periodically for evidence of runoff and erosion. Runoff undoubtedly occurred from the plots when the rainfall was intense but no evidence of erosion appeared on any of the plots that had mulch. The bare plots showed erosion in early fall following the first rain especially if that rain was intense (Figure 6). Within 3 or 4 weeks after the soil was wet, the new plants had grown enough to protect the soil and no further evidence of erosion was noticed. For the conditions of this experiment mulch was important in reducing erosion only until the new crop of plants had covered the soil.

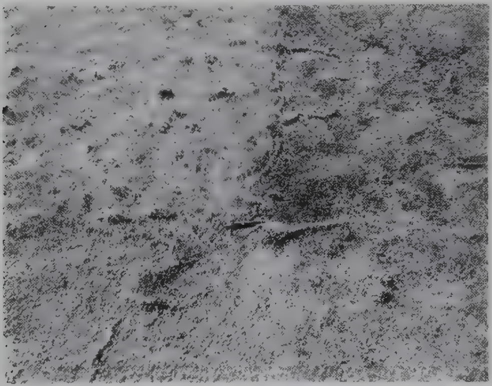

Fig. 6. Small terraces of soil and fine mulch washed from a bare plot during a storm of high intensity on October 18, 1953. Movement of materials was not obvious on the plots with a mulch cover.

Discussion

On the basis of this experiment, there seems little doubt that the amount and position of mulch in the California annual-type grassland are important factors which influence botanical composition and speed of plant growth. Since the latter two items are useful in the evaluation of the influence of grazing, determinations and interpretations of mulch effects should also be of value. The phase of range management most likely to benefit is that involving determination of forage utilization by livestock and the establishment of proper use standards. The concepts of current forage utilization, standards of proper use, and mulch are closely related. Utilization refers to the amount or percentage of current growth actually removed by the grazing animals. Proper use means utilization that will allow for continued high forage production. The portion of the herbage crop that remains after grazing on grasslands is mulch.

In studying and measuring utilization, the question arises as to whether emphasis should be placed on the portion of the forage eaten by livestock or the portion which is uneaten. Unfortunately, consumed forage cannot be measured directly. Therefore, attempts to measure the animal diet usually depend upon differences of measurements taken before and after grazing or under grazed and ungrazed conditions and upon conversion techniques. Inaccuracies seem to be inherent in these techniques so none of them have been accepted entirely.

The problem of determining the diet of a grazing animal is worthy of attention *per se*. One should know what plants in what proportion constitute the feed. These are important in the animal as well as in the plant aspects of range management. However, emphasis in the concept of utilization may be given in another way as illustrated by the question: How much plant material must remain to insure maintenance of forage production? This is conveyed in proper use standards but they are usually given in terms of the percentage of the crop which must remain after grazing. The results of this experiment suggest that it is the absolute amount and position of the material itself that is important rather than the percentage of the crop for the California annual type.

If the emphasis were put on the amount of plant residue needed to maintain production, then the measurements become straightforward. In this approach the procedure would be to describe proper use and adjust stocking on a basis of the material remaining (mulch) rather than on the material removed. The standards of proper use can be detemined by experimental procedures in direct terms such as weight of mulch per acre and percentage of soil covered at certain times of year. The standards would be the amounts of mulch needed to maintain production, promote ideal botanical composition of the ranges, and provide for adequate soil condition. Once these are determined, the field application becomes a direct sampling process. This approach was suggested by Dyksterhuis and Schmutz (1947) and expanded by Hyder (1954) on a basis of logic.

Forage plants in the California annual type are small, very close together, and annual. The vegetation contains many species which vary greatly in percentage composition from year to year. They also respond rapidly to varying amounts of mulch present at the beginning and during the growing season. The conventional methods of determining proper use and measuring utilization in other vegetational types are difficult to use. For these reasons, the "mulch" approach to help guide management of the California annual type may have considerable merit.

The finding that position or height of mulch is a factor in promting plant growth suggests that grazing should not be excessive and that animals should not be placed on a range of the California annual type in large numbers in order to remove all the harvestable forage in a short time. Grazing over a long period of time will allow animals to select the most palatable kinds of plants and plant parts. The mulch remaining after grazing would be composed largely of coarse stems and other materials high in fiber. Thus, moderate yearlong grazing would allow the animals to harvest the best forage and at the same time leave a favorable mulch cover.

SUMMARY

1. Amounts and position of natural mulch were manipulated according to 8 treatments and 8 replications for a period of 4 years. Yearly production of herbage was on oven-dry weight basis determined by sampling square-foot plots. Botanical composition, ground coverage and height of plant materials were determined by the point system.

2. A total of 46 species was found in the study area. Sixteen of them were alien and 40 were annual. Six species that were both alien and an-annual contributed between 67 and 84 per cent of the composition during the 4 years of the study.

3. A perennial bunchgrass, *Stipa pulchra*, increased in numbers from none to 612 plants within the exclosure between 1952 and 1955.

4. Amounts of mulch in the different treatments varied between zero and nearly 5,000 pounds on an acre basis. Not all of the mulch decomposed each year so there was a gradual accumulation from 1952 to 1955. The percentage increase was relatively greater where a larger proportion of current growth was left on the plots than where small amounts remained. The increase in percentage of the soil surface covered with mulch in each April from 1953 to 1955 also indicated accumulation of mulch.

5. With increasing amounts of mulch on the soil immediately before the fall rains, there was an increase in herbage production the following spring. This relationship is expressed by the regression equation $Y = 1214 + 0.354X$ for production within the 1,200 to 2,400 pound range.

6. *Baeria chrysostoma* responded quickly to the mulch treatment and after 1953 it was very abundant with no mulch and absent where mulch was the heaviest. *Aira caryophyllea* reacted in a similar fashion except it did not show significant differences between treatments until 1954 and the trend was still developing in 1955. Several other grasses and broadleaved herbs followed these same trends although to a much less degree.

7. *Bromus mollis* was the only plant that increased a significant amount in percentage composition with the heaviest mulch treatments. It is the species which contributed most to the high production.

8. The legumes and several additional grasses including *Festuca dertonensis* were most abundant on intermediate treatment. However, these differences were not significant.

9. Differences in the proportions of *Erodium botrys* due to treatment were not conclusive. However, this species and all others tested showed highly significant differences between years. Studies on the natural vegetation in the California annual type should include a measure of the variation resulting from different yearly environments. Otherwise, these may overshadow or confuse the differences due to treatments.

10. The proportion of the soil surface covered with moss varied significantly between years and to a less extent between treatments.

11. The height reached by *Bromus mollis* in the fall after the first effective rain and before cold weather was dependent upon the amount of mulch and the height of stubble (position of the mulch).

12. The average height of plant materials was determined by measuring the height of the first hit of the points above the soil surface. Significant differences in height of vegetation occurred between years and between treatments within 1954 and 1955. Both yearly and treatment differences in height undoubtedly reflect the differences in botanical composition.

13. The total percentage of ground covered by vegetation was related more to differences between years and and between locations than it was to differences in botanical composition between treatments.

14. Soil movement during the first intense fall rains and frost heaving were observed only on the plots where all mulch was removed each year.

15. The use of mulch in the appraisal of proper utilization of the annual range by livestock is discussed.

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USE OF OFFICIAL WEATHER DATA IN SPRING TIME—TEMPERATURE ANALYSIS OF AN INDIANA PHENOLOGICAL RECORD

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Introduction

Many statements might be quoted stressing the limitations of official U. S. meteorological records for ecological use. Also, the method of summation based on these or similar data has seldom found favor among ecologists, although it has recently proved successful in predicting the harvest date of peas (Sayre 1953) and is being used by truck-farming corporations for various crops. Nuttonson (1955) reviewed the literature, largely Russian, on wheat phenology, and extensively applied the conventional "remainder-index" method of summation, based on monthly means, to winter and spring wheat. Andrewartha and Birch (1954) criticized the summation idea, on theoretical grounds, for animals.

It seemed to the writers that new methods of treating Weather Bureau climatological records might be discovered which would give the massive, geographically widespread, long-continued, and readily accessible data an increased value for a number of purposes in plant and animal ecology and in agronomy. With this object in view, the statistical study here reported was undertaken jointly by the authors, representing pure and applied science fields, respectively.

The late Charles C. Deam, author of "The Flora of Indiana," kept careful records of the dates of first spring flowering for the plants in his private arboretum and garden at Bluffton, Indiana, from 1920 through 1952. Records are meager for the first few years while plants were being established, but *Sanguinaria canadensis* is recorded for 30 years and some others almost as long; these are therefore remarkable data compared with other American phenological records of native species. Other features are the authoritative identification and the fact that, for most of the woody plant species, all the annual dates refer to the same individual specimen, and to a clone for many of the herbs. This is the first published report involving the records, except for a mention of temperature effects on *Cercis canadensis* L. in a paper by Plummer and Lindsey (1955).

The Deam Arboretum comprised 3 acres at the outer portion of the Wabash River flood-plain at the west edge of Bluffton, Indiana. The soil type is Genessee silt loam. Dr. Deam recorded the date of first flower-opening at about 8:00 a.m. each morning when at home; he made no climatological records. The Bluffton Water Works, adjacent to the Arboretum on the east, initiated a meteorological station in cooperation with the U. S. Weather Bureau and obtained unbroken records for 1949 through 1952. For the years 1920 to 1940, good records from another weather station at Bluffton are available. However, because satisfactory weather records were not made at Bluffton from 1941 through 1948, the phenological records from this period have not been utilized for the principal analysis in the present paper. The plant names herein are those used by Deam (1940).

The long-continued meticulous observations by Dr. Deam and his kindness in furnishing his records for analysis have made this report possible. Word of their existence and help in obtaining them had come from Prof. Daniel DenUyl. Prof.

S. R. Miles, statistician of the Purdue Agricultural Experiment Station, gave valuable mathematical advice and authorized much preliminary computation by his technicans during the testing of various tentative methods which are not detailed herein. The mass of the statistical computations was made by punchcard machines in the Purdue Statistical Laboratory; 5,500 cards were needed.

The basis of selection of the spring temperature factor for study

The opening of the flower is an observed endpoint preceded by a complex of chemical and growth processes which are little understood. Lang (1952) stated that "our insight into the later stages of flowering is very deficient." The present study does not attempt to segregate the numerous possible environmental variables and different means of expressing them for individual consideration. The aim is to consider the influence of temperature over the period of February 1 to May 15 to find a suitable quantitative means of integrating and expressing its operation. Statistical study of such data reveals the manner in which the temperature factor influences the series of changes culminating in flower opening under outdoor conditions. However, certain other possible factors may be briefly discussed in order to show their lesser significance in affecting flower opening under the given conditions, or unsuitability for study under the circumstances.

Although low winter temperatures are required by many plants for later spring growth, it was assumed that outdoor minimum temperatures in northern Indiana are sufficiently low, and no study was given to the possible effect of this factor on the spring flowering date.

Most of the knowledge of the physiology of reproduction in angiosperms concerns the initiation of flower primordia. This has little bearing on the present problem because in all the native woody plants and practically all of the herbaceous perennials recorded by Deam, the flower buds are already formed before the advent of fall dormancy. Moreover, photoperiod is not an important variable in this case; obviously, if flowering date were controlled only by the astronomically determined day-length, an individual would flower on the same date every year. The wide deviations from the average date over many years show the controlling effect of a factor or factors other than photoperiod. Went (1953) stated that plants in which flowering is controlled by day length are mostly annuals, while in bulbous plants like hyacinth, tulip, narcissus, Easter lilies, and onions, temperature is a major factor which controls their flowering. The herbs grown in the Deam Arboretum were all perennials.

Another possibility, that flower opening could be most influenced by impinging radiant energy, might mean that the best meteorological expression for the purpose would be total hours of sunshine rather than air temperatures. Some investigation of this was made, using "per cent of possible sunshine" from the first order U. S. Weather Bureau station at Fort Wayne, 17 miles from Bluffton. For each day from March 1 to May 15 for each year available (*i.e.*, from 1940 to 1952), this was multiplied by the minutes between astronomical sunrise and sunset for the latitude of Bluffton and the product converted to hours. Coefficients of variation of these summed hours of sunshine for the years of record showed that 4 of the 5 species used were much more affected by air temperature than by sunlight. (One species showed about equal influence.)

A cold, clear day may be ineffective in early spring, whereas a warm, clear day may be more effective than temperature alone would indicate. If sunshine alone is considered, a warm, cloudy day would not be counted as more effective than a cold, cloudy day, even though actually much more so. A daytime temperature figure would often reflect some of the influence of sunshine, whereas an expression for sunshine alone fails to incorporate the air temperature factor. Since preliminary study indicated that precipitation and duration of sunshine were less important, further work was confined to temperature alone.

METHODS

Preliminary steps involved plotting, for 51 species of Deam's phenological record, the mean day departures from normal blooming date for plants that normally bloomed between March 1 and May 1. Few bloomed in March. On the same graph were plotted the mean departures from normal temperature. For this purpose, the full period 1923 to 1952 was used; weather records for 1940 to 1948 were taken from Berne, the nearest station furnishing continuous records, 15 miles from Bluffton. This graph (Figure 1) shows good inverse correlation between flowering date and temperature, *i.e.*, high temperatures were clearly associated with early flowering, low temperatures with late. In a similar graph (not shown) using spring precipitation instead of temperature, slight correlation of current precipitation with flowering date seemed possible, since in 15 of the years high precipitation went with early flowering and low with late, although in 10 other years high precipitation was associated with

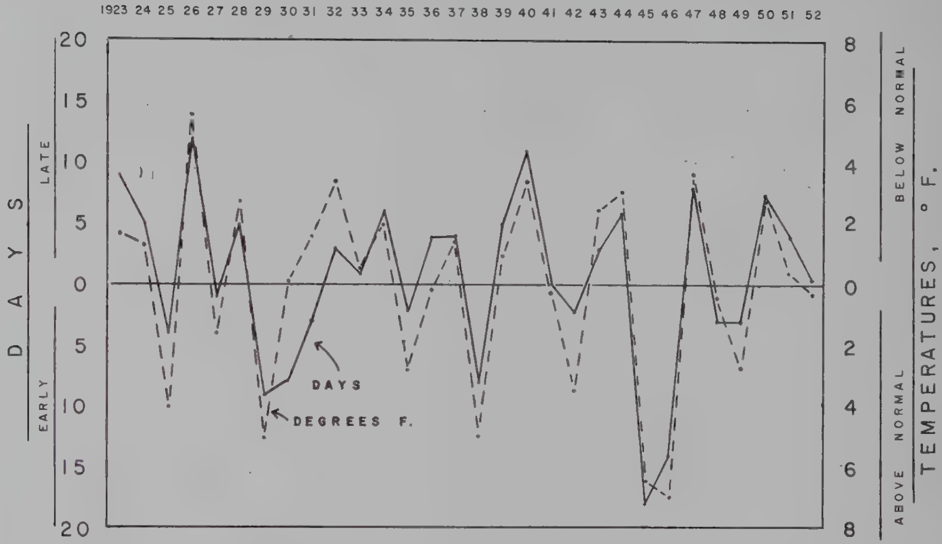

Fig. 1. The heavy curve shows the average number of days in each year by which the flowering dates of 51 species that flowered normally before May 1 were earlier (below solid abscissa line, 0) or later (above) than in the statistical normal year (0). The dashed curve shows the averages of daily departures (from March 1 to May 16) from daily mean temperature. Above-normal departures were plotted below the "normal" abscissa (0), below-normal departures above it. Temperature data were obtained at Bluffton, Indiana, for 1923-1940, and from Berne, 15 miles away, for 1941-48.

late flowering and low with early. These graphs lent distinct encouragement for further analysis to determine a suitable expression for the temperature factor, which would lead to an understanding of its mode of operation in influencing flowering dates.

As noted above, previous workers have indicated that temperature summations based upon daily means are inadequate. The main reason is that the daily "mean," which is actually the median of the minimum and maximum, fails to take into account the *duration* of the various temperature levels during the daylight and night hours. For example, if 55° F. were the threshold below which the processes that culminate in flowering were not occurring, it would make no difference whether the temperature on a given day dropped to 54° or to 36°. But it would matter how long temperatures between 55° and the maximum prevailed during the 24-hour period. Again, if development within flower buds proceeds most rapidly at 80° F., it is less important that the maximum reached 80° than whether it stayed between 70° and 80° for one hour or six.

Since available temperature records provided only the maximum, minimum, and mean, it is obviously impossible from these to get at the duration factor directly for a particular day. However, if daily temperature curves in spring fluctuate around an average pattern in a normal rather than a bimodal distribution, it should be possible to determine the degree-hours (taking account of the duration factor) of a typical or average day for each combination of maximum and minimum. Continuous 7-day tracings of temperature from recording thermographs in the Ross Biological Reserve near Lafayette were studied for the spring months of several years. Although the flatter, narrow-range tracings of low-pressure days and the sharp peaked tracings of high-pressure days were distinguishable, more of the days were intermediate in character so that the frequency curve of the types of diurnal temperature pattern was a normal, unimodal curve. Thus, days which deviate in one direction from the average diurnal pattern tend to cancel out those days deviating in the other direction, and the statistical average day is a satisfactory basis of computations in a study dealing not with isolated individual days but with degree-hour summations over a long period including days of the three main types and the gradations between them. The advantage of the statistical time-temperature concept over the method of summing the means themselves, or summing temperatures above a daily mean used as an assumed threshold, is brought out in the description which follows.

Figures 2, A-D, are presented to clarify this new approach to daily temperature effectiveness. They do not depict actual or idealized temperature curves, but are geometrical abstractions to illustrate derivation of the formulae which provide the daily degree-hour figures used for summing. The base line is 24 hours long. The temperature is always at or above the low (w) for the entire 24 hours. Since this cannot be true of any other temperature point, a triangle with this daily low (or the threshold temperature t, whichever is higher) as a base is drawn to the high (h) as the apex, because all temperatures below the high are maintained or exceeded for a longer time than the high is maintained. This triangle represents part or all of the effective degree-hours during that day.

If the threshold is below the low, as in Figure 2, A, the time-temperature between these figures must be taken in account. This forms a rectangle representing another 10 degrees lasting the whole 24 hours, yielding 240 degree-hours. Adding the triangle above, it totals 720 degree-hours for the day. In view of the above relationships the formula for effective degree-hours in one such day is

$$24\ (w - t) + \frac{24\ (h - w)}{2}$$

The dashed rectangle represents the degree-hours computation based on the daily mean (m), also 720 in this case. This is explained by fact that the two stippled triangles on the left are equal in size, as are also the two corresponding ones on the right. Thus, the much simpler formula (m — t) 24 yields the same degree-hours figure. This holds true when the threshold is either below the low (Fig. 2 A) or equal to it (Fig. 2 B). In the latter case, the solid line forms a triangle only, but this equals the dashed rectangle based on daily mean.

On the other hand, whenever the threshold exceeds the low, the use of the mean is unsatisfactory. In Figure 2 C, t is between the low and the mean. The stippled area of the rectangle equals only the stippled fraction of the upper triangle, while the unstippled isosceles triangle above is disregarded. By use of the mean there seem to be only 120 degree-hours, although there are actually 160 enclosed within the effective solid triangle for this day. The latter figure is obtained by a formula of which the derivation may be illustrated by Figure 2D if the letter m is disregarded.

Between the 24 hour base-line and the threshold level t, temperature is ineffective; only the area of the solid triangle is used. The threshold does not last for 24 hours, and the higher is t in relation to w and h, the shorter is the time at or above the threshold. The base at t is $\frac{h - t}{h - w}\ 24$, and the area of the solid triangle is therefore

$$\frac{h - t}{h - w}\ 24\ \frac{h - t}{2}$$

$$= \frac{12\ (h - t)^2}{h - w}$$

The higher that t rises in relation to m, the greater the discrepancy between the two methods, until t equals m (Fig. 2 D) and the former rectangle consequently has been flattened to a single line. In this case (and when t is higher than m), the discrepancy between the two methods is most extreme. Figure 2 D would show zero degree-hours by using the mean, (m — t) 24, while the correct formula, which is the same as for Figure 2 C, shows that the solid triangle contains 280 degree-hours. Since days with means equal to or below the threshold occur more frequently early in the growing season, the proposed method works best for spring-flowering species.

To summarize, use of the mean yields the true degree-hours value only when the threshold does not exceed the low. When the threshold is between the low and the high, use of the mean gives less than the true value. The most serious underestimate occurs when the threshold equals or exceeds the mean, because, in these cases, use of the mean gives zero. When use of the mean results in an underestimate, the greater the diurnal range the greater the underestimate. When the threshold is above the high, the true value is of course zero by both methods.

A master table was prepared. Instead of computing each degree-hour figure in the body of the table by the formula given earlier, the same results were obtained more quickly by building a series of preliminary tables, which need not be detailed here. Since the master table can be used for future studies anywhere based on the new degree-hour formula, copies have been filed with the Life Science Library of Purdue University and the United States Department of Agriculture Library in Washington. The table includes all the basic degree-hour figures (for a given combination of daily high and low) from which summations are made for the series of dates prior to the flowering date of a given species. For a given presumptive threshold, the headings across the top begin with this threshold. They are consecutive integers representing daily highs in degrees

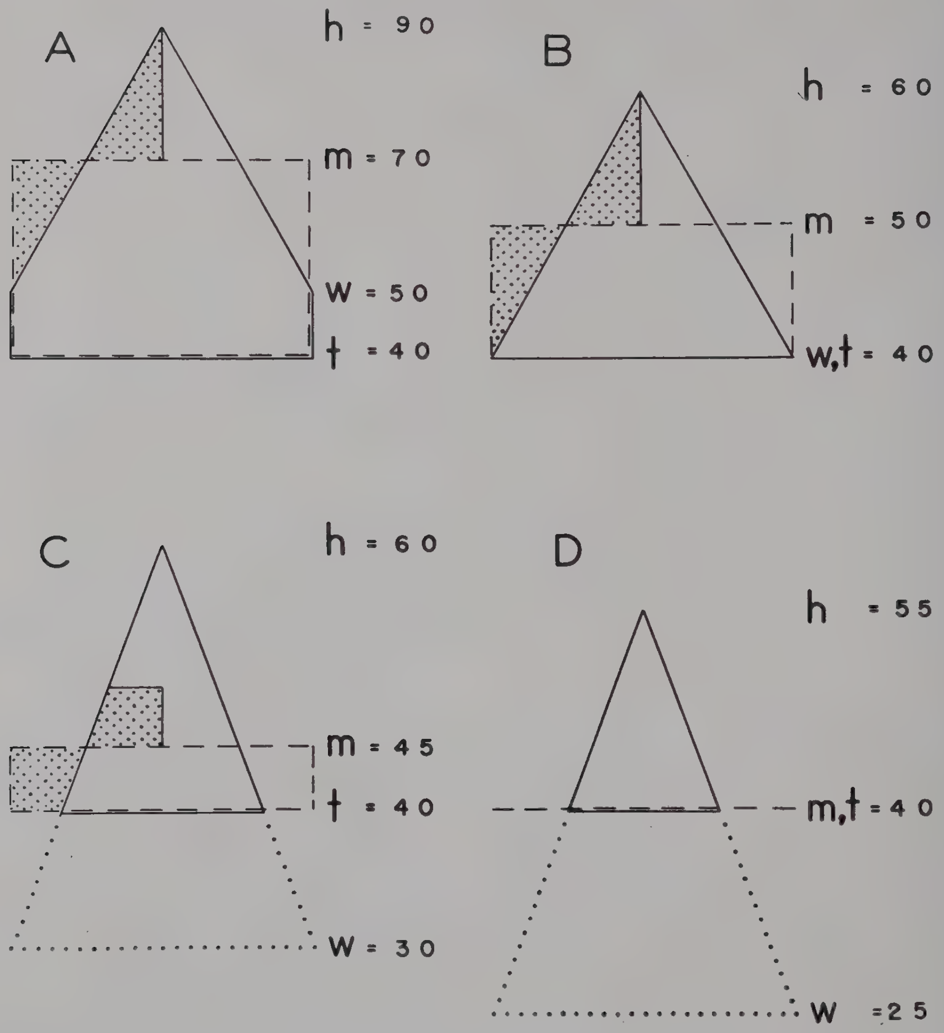

Fig. 2. Comparison of degree-hour areas by use of daily mean (m) in ordinary summation (dashed rectangles) and by use of the duration-summation method (solid figures), illustrating derivation of formula for the latter method (see text). Daily maximum temperature (h), mean (m), daily low (w), and meteorological threshold (t) are shown for each of four types of days. From A through D there is a progressive rise in the threshold relative to the other temperature points. The base line is 24 hours long. Stippled portions show equal time-temperature areas within a given day. Dotted lines enclose ineffective areas below the threshold.

Fahrenheit. The table headings down the side are consecutive integers for the daily lows, and cover a range of 65 degrees. Since 6 possible thresholds at 5 degree intervals were being tested for each species, 6 such large tables, in effect, were needed. However, the same base table was used for all thresholds. This was made possible by preparing substitute headings on paper strips for 5 of the 6 thresholds. For example, to shift the table for a 5 degree higher threshold, the new horizontal and vertical heading figures would be 5 degrees higher for any fixed point in the body of the table.

A series of tables was prepared from the U. S. Weather Bureau (1920-1952) climatological data, showing the high and low temperatures for each day from February 1 through May 31 for each year. In order to avoid inaccuracies due to leap years, flowering dates were numbered chronologically from March 1 as day 1, while negative numbers were assigned back from the last day of February with only February 29 as day zero.

By using these tabulated daily meteorological records against the master table, daily degree-hours above the various presumptive thresholds were obtained. These basic climatic data were punched into the first work deck of IBM cards which showed the degree-hours above 30, 35, 40, 45, 50 and 55 degrees Fahrenheit for each day from February 1 through May 31 during the 30-year period, 1923-1952.

Into a second deck were punched year, species code number, and flowering date; also the appropriate degree-hour figures of deck 1 were added and the sums obtained were punched into deck 2. This was done by taking a cumulative subtotal for each 10-day period backward from the flowering date, giving a basis for comparing effectiveness of different time periods: 10, 20, 30, 40, and 50 days, and a sixth category including all days back through February 1. Of course only those days having temperatures above the given threshold contributed to the summation value for that threshold category. It is significant that the threshold as used here is not a mean of any sort. From deck 2 a series of checking tables were printed to show the sum of degree-hours for each species, for each year of record, for each 10-day period cumulatively backward, for each presumptive threshold.

Deck 2 was used to prepare a summary deck (3) from which standard statistical computations were made for determining variance (s^2) among the degree-hours sums for the different years. In the last pass through the machine the mean sum and the standard deviation (s) for each species, at each time period, and for each presumptive threshold were printed as a final table. The latter included columns for species number, presumptive threshold, time period for each, years of record, mean degree-hours for a given combination of time and threshold, and standard deviation for the same combination. After the coefficient of variation (standard deviation as per cent of the mean) was recorded by hand as a last column, the table contained all the information about a species needed to determine its threshold temperature, time period of preflowering activity in spring, and requisite heat sum for flowering.

From these data, a table of coefficients of variation at different time periods and presumptive thresholds was made for each species. That for *Cypripedium calceolus* constitutes Table I. In any threshold column, the lowest per cent figure is in the row for 40 days prior to the flowering date, *i.e.*, the coefficient decreases with time to 40 days, then increases. Occurring with all thresholds, this is the clearest evidence of approximately 40 days as the significant time period for this species in an average year. (Similar evidence was found for various time periods in tables for 13 other species.) However, perusal of the horizontal row for 40 days or other time period shows a continuous trend from low coefficients at the left to high ones at the right. Since this holds true for all 24 species, threshold temperatures could not be conveniently determined from the tables directly.

TABLE I. Coefficients of variation for *Cypripedium calceolus* var. *pubescens* at various presumptive thresholds and time periods, indicating 40 days as the significant time period

Time in days	TEMPERATURE IN DEGREES FAHRENHEIT					
	30°	35°	40°	45°	50°	55°
10.......	19.5	23.5	28.5	33.0	38.7	45.9
20.......	16.5	20.0	25.3	30.4	37.0	44.8
30.......	13.5	16.7	21.7	27.4	34.5	42.2
40.......	*9.9*	*12.3*	*16.1*	*20.6*	*26.7*	*33.5*
50.......	12.8	15.6	19.3	23.4	28.9	34.8
60±.....	15.0	17.6	21.3	24.8	29.4	34.5

With progressively lower thresholds, the coefficient of variation decreases because the standard deviation (the numerator) increases less rapidly than the mean heat sum (the denominator). The inclusion, in the denominator, of noneffective heat units, which may be termed "padding," causes this decrease in the coefficient of variation to continue beyond the significant point. In time period determination also, the "padding" effect is strong enough to obscure the significant period in nine of the species. Wherever the curve for threshold or time period shows no minimum, inspection of the table fails to reveal the significant point; instead, graphs indicating the rate of change between points are required.

For each of the 24 species, 5 graphs were made. Each graph had 6 curves plotted with 6 points per curve, with the exception of one type which could not show a curve for the reference threshold of 30°F. The interpretation of the graphs is exemplified by those for leatherwood (*Dirca palustris*) one of the species for which the table of coefficients of variation was inconclusive. Thus, in Figure 3, a curve of standard deviation of the heat sums against days was plotted on semilog paper for each threshold in order to find which of the 6 presumptive periods is closest to the significant one during which occurs the spring activity that leads to flowering. If such a curve were due solely to the above mentioned "padding" effect, it would rise smoothly toward the maximum standard deviation for 60± days. Therefore, the pronounced dip, or displacement toward lower deviations in the threshold temperature curves in Figure 3 indicates 40 days as the approximate time period sought.

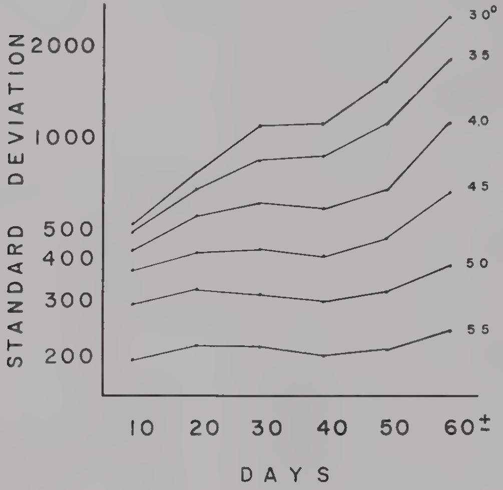

FIG. 3. Curves of standard deviations of 6 presumptive temperature thresholds for flowering of *Dirca palustris,* plotted on semilog paper against time in days. The significant time period (40 days) is indicated by downward displacement along that ordinate. (The period 60± days includes all days, from February 1 to the 50th day before flowering, that contribute heat above the respective thresholds.)

Figure 4 serves primarily to indicate temperature threshold. A curve of standard deviation against threshold was plotted on semilog paper for each period. The 10 days' curve is smooth because this short late period is far from the significant one, and its points controlled almost entirely by the "padding" effect. The other curves show a downward displacement of their 45° points, which is therefore the threshold for this species. The drop in deviation at the 45° ordinate is especially marked on the curve for 40 days, which was the period determined as significant from Figure 3.

The two graphs for *Dirca* shown in Figures 5 and 6 are for the coefficient of variation and are plotted on arithmetic paper. The coefficient of variation is the standard deviation as a per cent of the mean. Since the coefficients increase from below upward, a downward displacement indicates significance. In Figure 5, the curve for 45° and curves for all lower temperatures show a definite displacement on the 40 day ordinate. In Figure 6, there is a similar break in the curves for 20, 30, 50, and especially 40 days, on the 45 degree ordinate.

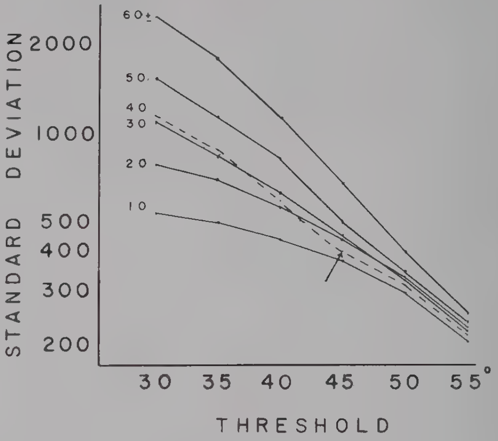

FIG. 4. Curves of standard deviations of 6 presumptive time periods (in days) of pre-flowering development for *Dirca palustris,* plotted on semilog paper against temperature in degrees F. Arrow shows the significant threshold ordinate (45° F.).

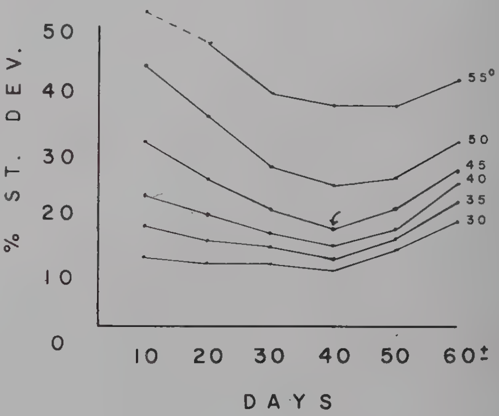

FIG. 5. Curves of coefficients of variation (standard deviation as per cent of the mean) of 6 presumptive temperature thresholds for flowering of *Dirca palustris,* plotted against time. Arrow shows significant time period ordinate (40 days).

In a fifth graph (not shown) for *Dirca,* also on arithmetic paper, the rate of change among standard deviations was compared. Each plotted point is the percentage that a given standard deviation is of the (higher) standard deviation of the next lower presumptive threshold. Curves for periods are plotted against thresholds on the base line. Since the longer time periods have the lower

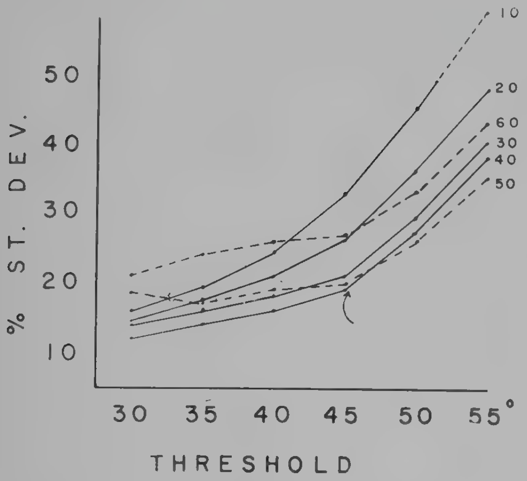

Fig. 6. Curves of coefficients of variation of 6 presumptive time periods for flowering of *Dirca palustris*, plotted against temperatures. Arrow shows significant temperature threshold ordinate (45° F.).

standard deviations and the lower percentage change, a downward displacement from the expected "padding" curve indicates the ordinate of the significant point. The most striking displacement occurs on the 45° ordinate. This is especially true for the curve for the 40 day period. Thus, this graph supports the conclusions based on other graphs in which standard deviations and coefficients of variation were plotted as curves for both periods and thresholds.

For direct verification of the duration-summation formula, values from the master table were tested against actual counts of degree-hours from recording thermograph sheets. The record, covering February 1 through May 24, 1953, was made in a standard cotton-belt instrument shelter under the closed canopy of an oak-hickory forest. The degree-hours above 40° F. and below the ink trace were counted for each day, and cumulative monthly heat sums thus obtained. The latter were compared with similar figures from the summing of daily heat sums based on daily maxima and minima from the same thermograph tracings, and derived from the master table. For the 4 days in February exceeding the 40° threshold, the sum by use of the master table was 2.7 per cent high. It was 3.8 per cent high for February and March together. By the end of April, the cumulative heat sum was 2.6 per cent high, while for the entire February 1-May 24 period the table gave a value only 2.6 per cent above that from the actual count. If proposed future comparisons show such a consistent bias in spring for various places, years, and instrument heights, applying a small correction factor to the present table should yield accurate estimates of heat sums (prior to given phenologic events) from ordinary maximum-minimum weather data, and may simplify collecting data in microclimatic ecology. In contrast, the same 1953 thermograph sheets interpreted by the traditional summation formula (m — t) 24 gave a heat sum too low by 45 per cent for February, by 19.8 through March, 34.4 cumulatively through April, and 44.6 for February 1 through May 24.

Results and Conclusions

The general results are summarized in Table II in which species are given in sequence of flowering date. The 8 years of Berne temperature records were used only for Figure 1 and the first two columns of Table II; in the principal analysis, using Bluffton records, the species ranged in number of years from 11 through 22.

In certain species, interpretation of significant points from the graphs was somewhat questionable. Probably this is due to an unusually slow start of spring activity, the true growth curve in these plants rising very gradually from its base line, presumably in a curvilinear form. The threshold given for the following species in Table II was questionable: *Prunus tomentosa, Amelanchier humilis, Aesculus glabra,* and *Caragana arborescens.* Determination of number of days was more clear cut generally, but there was some question about correctness of growth periods for *Claytonia virginica, Cercis canadensis,* and *Mertensia virginica.*

The time span of mean first flowering for the species studied covers 46 days. Of the 10 species which flower during the first half of this time, on or before day 50, 70 per cent have the lowest threshold, or 40° F. Of the 14 species flowering in the last half, only one species (7 per cent) has a 40° threshold, while 28 per cent have the highest threshold, or 50° F. The earlier group has 60 per cent, and the later group has half, of the species with one of the two shorter time periods, 20 and 30 days. Twenty per cent of the earlier group require 50 days of development, as compared with 7 per cent of the later group.

Considering only the herbs, 43 per cent of them had the 40° threshold, another 43 per cent had the 50°, and only 14 per cent had the average or 45° threshold. All the shrubs studied had the 45° threshold; half of the trees had 40° and the other half 45°.

The herbs were grouped into early (day 50 or before) and late flowering species. Forty-three per cent of the herbs had both the 40° threshold

Table II. Flowering statistics for 24 species. Years of record and flowering dates range based on years 1923-1952. Other columns based on 1923-1940 and 1949-1952 when usable U. S. Weather Bureau Records were made at Bluffton, Indiana

	Years of record	Range of first flowering date, in days	Mean flowering date from March 1	Threshold °F	Growth period days	Mean degree-hrs. sum	Per Cent Departure From Mean Sum	
							Early yrs.	Late yrs.
Trillium nivale Riddell	27	27	27	40	40	2557	+15.3	−18.3
Hepatica acutiloba DC.	20	29	34	40	30	3235	+13.5	− 7.2
Dirca palustris L.	25	34	36	45	40	2128	+ 8.4	−10.0
Claytonia virginica L.	26	34	40	40	20*	3116	+ 3.6	− 0.4
Sanguinaria canadensis L.	30	30	44	40	30	4304	+16.0	− 3.5
Isopyrum biternatum (Raf.) T. & G.	24	34	45	40	30	4634	+ 9.3	− 6.6
Prunus tomentosa Thunb.	23	34	47	40*	30	4816	− 3.0	+ 3.3
Jeffersonia diphylla (L.) Pers.	25	39	48	50	50	2034	− 8.3	+ 9.1
Dentaria laciniata Muhl.	19	28	50	40	20	4511	+11.2	− 8.5
Dicentra cucullaria (L.) Bernh.	25	31	50	50	50	2339	+ 7.4	− 4.1
Stylophorum diphyllum (Michx.) Nutt.	25	30	51	50	30	2107	+ 0.2	+ 8.0
Lonicera canadensis Marsh.	23	37	52	45	20	2790	+ 8.1	− 4.7
Amelanchier canadensis (L. Medic.)	17	37	53	40	40	7211	− 6.9	+ 2.6
Mertensia virginica (L. Link.)	23	31	54	50	40*	2817	+ 7.2	− 3.2
Ribes odoratum Wendl.	17	40	55	45	30	3962	− 5.2	+11.7
Hydrastis canadensis L.	24	26	56	50	50	3684	+ 0.8	+ 0.9
Uvularia grandiflora J. E. Smith	25	23	56	50	20	2134	+15.5	−12.7
Amelanchier humilis Wieg.	22	24	60	45*	40	5798	+ 0.4	+ 0.5
Aesculus glabra Willd.	17	35	61	45*	40	6878	+11.1	− 2.5
Cercis canadensis L.	18	33	61	45	30*	5020	− 8.6	+ 2.1
Caragana arborescens	19	28	65	45*	20	4720	−14.3	+ 3.8
Staphylea trifolia L.	18	36	66	45	20	4685	− 3.5	+ 0.2
Aquilegia canadensis L.	18	25	69	45	40	8533	− 5.5	+ 5.7
Cypripedium calceolus var. *pubescens* (Willd.) Correll	16	20	72	45	40	7998	+ 8.6	+ 0.2

*Questionable figures

and early flowering, while no herbs combined this low threshold with later flowering. Again, 14 per cent of the herbs have both the 50° threshold and early flowering; while 29 per cent have this high threshold and flower after day 50.

Both of the 45° threshold herbs had the 40 day time requirement. All the shrubs had the 45° threshold; 50 per cent of them required only 20 days, 17 per cent needed 30 days, and 33 per cent 40 days. None of the 45° species of any life form required 50 days.

Herbs having 20 or 30 day growth periods were considered separately. Thirty-six per cent of the herbs combine one of these short periods with a low 40° threshold and early blooming date, while no herb had this same time period and threshold and bloomed late. No species combined the 20-30 day period with both 50° threshold and early date, but 14 per cent of the herbs shared this short period and high threshold with blooming date later than day 50. In other words, all short period plants (regardless of life form) which had the highest threshold, bloomed during the last half of the flowering date span observed.

Twenty-one per cent of all herbs had both a 50 day growth period and a 50° threshold. No 50 day herb had any other threshold. There were no shrubs or trees with a 50 day growth period.

Short time periods, then, are associated with low temperature thresholds and early blooming dates, whereas long periods are associated with high thresholds and late blooming dates. In comparing the earlier with the later-flowering group, the higher heat sum for the latter indicates their requirement for the increased heat accompanying the advance of spring. Despite a higher mean threshold and almost equal mean period, the degree-hour sums average higher for the later-flowering group. Separating the life forms, the average flowering date for herbs was considerably earlier than that for shrubs or trees, and the heat sum for herbs lower. The two latest plants studied, the herbs *Cypripedium* and *Aquilegia*, had the two highest heat sums. In both, considerable vegetative growth is needed before flowering. Late flowering plants may not have higher thresholds or longer time periods, but usually have higher heat sums. This requirement of more heat units necessitates late blooming if other factors remain constant.

Table III shows the mean date, threshold, time period, and heat sum for each life form. In comparing species having the same flowering date, a larger heat sum may be brought about by either a lower threshold, or a longer time period, or both. With the same thresholds and the same heat sums, which is essentially true between the herb and shrub group, a later flowering date must be associated with a shorter growth period. For both herbs and shrubs, the mean threshold was 45° and the heat sum about 3900, yet the shrubs averaged 6 days later, and had a 6.7 days shorter time period. Thus, the mathematically determined period fits the actual time difference. This is one indication that the threshold figure being obtained is the meteorological threshold that applies *daily* when rising or falling temperature crosses that level, rather than the temperature required to initiate spring growth. These are not necessarily the same temperatures, and may be very different.

TABLE III. Averages for herbs, shrubs, and trees separately. Flowering date numbers begin with March 1

	Mean flowering date	Mean threshold	Mean time, days	Mean heat sum
Herbs.......	50	45	35.0	3857
Shrubs......	56	45	28.3	4014
Trees.......	55.5	42.5	35	5981

In addition to flowering date, threshold, and time period, the life form or stature must influence the heat sum figure for a given speces. While the average flowering date for herbs was day 50, that for shrubs was 56, and for trees 55.5. Two species having the same threshold and time period do not have the same degree-hours sum unless they flower on the same date. The later of two such plants would have the higher sum, as indicated above. The trees used apparently require a considerably higher temperature sum for flowering, even though less new vegetative growth is built up prior to flowering than in the herbs. That portion of the difference in heat requirement which brings about later blooming is undoubtedly real; however, another part of the heat sum figure is merely apparent, being caused by the greater height of flower buds incident to the tree life form. The actual temperature immediately surrounding the bud would usually be lower in spring than that recorded in the instrument shelter only 5 feet above ground. This would contribute a higher sum for trees. For this reason, the threshold temperature is regarded as a meteorological threshold value rather than a physiological one.

Conversely the herbs, many of which flower before trees leaf out, probably received slightly more heat than was indicated in the record, tending to lower their sums. Thus, the use for all life forms of the same records from a standard shelter makes the effective degree-hours somewhat relative to the life form and stature of the species. Shrubs are similar to herbs in stature (and hence in amount of heat actually received), but to trees in that little vegetative growth is prerequisite to flowering in a given season. In the shrubs, the combination of equal blooming date and very short time requirement decreases the sum below that for trees. Herbs start activity much earlier than woody plants, but the first growth is usually vegetative. In all the trees used except *Aesculus,* little vegetative growth precedes flowering.

DISCUSSION

It is desirable to compare the heat sum (Table II), which is a mean of sums in all recorded years for the given species, with the mean of heat sums for only those few years when the species flowered on its mean flowering date (Table II, third column) or on the day before or after it. From 2 to 5 years were available for computing the restricted mean, so that it varies considerably in accuracy. However, the generally good correspondence between the two means increases confidence in the duration-summation method. In the 18 species for which two or more normal or practically normal flowering years were recorded, the two mean heat sums differed by less than 1 per cent (of the overall mean) in 2 species, less than 2 per cent in 3 other species, 3 per cent or less in 4 other cases, less than 4 per cent in another, 6 to 8 per cent in 2 others, 11 to 15 per cent in 3 others, and 16 to 20 per cent in the remaining 3 species.

Another instructive comparison is that between heat sums for early versus late flowering years (Table II, last two columns), disregarding the 3-day period centered on the mean flowering date. Since the positive and negative departures from the overall mean heat sum might be expected to approximately balance, the decidedly skewed distribution calls for interpretation. The fact that 16 of the 24 species had positive departures for the years of early blooming indicates that one or more environmental factors in addition to air temperature probably help determine flowering date. Examination of the two columns suggests why more heat units are required by the same plant in years of early blooming. Of the 12 species which normally flower before day 53 (April 22), all but two show a higher heat requirement in early years. One of the two which does not is a tree. Six, or half, of the species normally flowering on or after day 53 show no increased heat requirement in early years, but all except one of these is a woody plant. Trees and shrubs have deeper root systems than herbs, and also may contain enough water in early spring so that flowering does not depend on absorption by the roots, as does growth of the aerial part of an herb and its flowering. The higher heat sums in the 12 earlier species may occur because surface soil temperatures lag farther behind rising air temperatures in early years than in normal or late ones. This would be expected since soil temperature is much affected by direct insolation. Despite the abnormally high shelter temperature (at a given date) in an early year, the shorter day and lower insolation angle causes a greater lag (at a given stage of plant development) in temperatures of the surface soil and the air just over it, than in a late year. In compensation for this, shelter temperatures must be high enough to give a heat sum in that year higher than the mean sum of all years. As the table shows, perennial herbs are more subject to this effect than woody plants, and early flowering plants more than later ones. In late years, the early flowering plants, especially, benefit from the abnormally (for a given phenological stage) warm surface soil and adjacent air, so that they require less heat as indicated by air temperatures farther above the surface.

The complexity of ecological problems has brought about the acceptance of indices and integrating expressions. Our use of temperature alone does not signify adoption of a one-factor viewpoint; it is probable that the degree-hour figure as here computed integrates to some degree several related factors affecting the plant simultaneously. An analogous case is found in the use of the atmometer, which does not measure wind, temperature, and air humidity individually, but integrates their combined effects into a single meaningful empirical index for expressing evaporativity. The careful laborious measurement of each factor separately does not make possible computation of a more valuable figure for evaporativity; in fact, this greatly increases the difficulty of interpretation.

During the diurnal march of temperature, plant activity begins when the increasing temperature as recorded in the standard shelter reaches a given point, the meteorological threshold temperature. It need be considered only for those days when rising or falling temperature crosses the threshold value. Consequently, in early spring when the high remains below the threshold, and later during days when temperatures are constantly above this value, the threshold has no effect. The term threshold in this sense applies to many successive days of spring for an individual plant; it does not necessarily refer to the temperature at the one time each year when growth is initiated following the winter dormant period.

According to Lang (1952), ". . . the development of the different parts of a flower is highly coordinated and if conditions are unfavorable all parts cease growth simultaneously." This would occur when shelter temperature falls below the meteorological threshold.

Because of the relation between life form of the species and conditions of the instrument installation, the concept of meteorological rather than physiological threshold is applicable. The latter would require measurements within the bud itself. Under the circumstances of the present study, as with most ecological work, only a meteorological threshold is feasible to study. Temperatures in the shelter, while not identical with those affecting the plant, parallel them closely enough to be ecologically useful. The average meteorological threshold determined herein is slightly higher than thresholds determined by physiologists in constant-temperature experiments. Both methods have certain disadvantages. In this study, a species threshold should be relatively constant while the time period may vary widely from the listed mean, depending on the season.

Although it is likely that a curvilinear temperature-growth relationship obtains, most applications of the summation concept have assumed some sort of linear relationship above the threshold. Efficiency indices based on the Q_{10} idea were tabulated for each degree, from a 40° F, threshold through the 99° level, by Livingston and Livingston (1913). The assumption of a linear relationship underlies the present study. The latter is not based on Q_{10}, but takes into account the approximate duration of each temperature level throughout the 24-hour day. Information is lacking as to when and how the accelerating effect of increasing temperature levels may apply to native spring-flowering species, and it is not well understood even for crop plants. Went (1953) stated, "Work of a large number of investigators . . . indicated that as an organism . . . is subjected to a gradually changing temperature, its temperature coefficient changes." There appears to be insufficient basis for use of the Q_{10} concept in an empirical approach dependent on a rather rough correspondence between temperature as recorded and that affecting flower development. Also, it seems better to use a constant linear relationship than to apply some arbitrarily selected curvilinear refinement to all the diverse species involved.

Of the cardinal points, optimum temperature has been most investigated. This is because quantitative studies can be based upon yields of plant products, which serve as a measure of the optimum. The growth minimum or threshold is not expressed in yields and has been little studied, but is of much phenological interest.

The average threshold value of all species found in this study compares closely with results of those using other species and methods. The heat sum results show inherent consistency and lend themselves to reasonable interpretation. The duration-summation method using official U. S. Weather Bureau data appears to be a useful tool for phenological research. If taken at one place, phenological records must cover a long series of years to be of value; however, short-term studies could apply the method by using a number of different stations. By either approach, abundant data are required because the method is not sufficiently sensitive to interpret a short series of flowering dates. Data could be collected cooperatively at various pure and applied botanical institutions, such as the arboretum, botanical garden, and agricultural experiment station. Other phenological events than flowering might be studied.

SUMMARY

Dr. C. C. Deam observed dates of first spring flowering in his arboretum and garden at Bluffton, Indiana, from 1920 through 1952. This record was analyzed in connection with temperature data published by the U. S. Weather Bureau from Bluffton. For preliminary guidance, 51 species were averaged, and for each year, departures from normals in flowering date, daily mean temperature, and spring precipitation were compared. Temperature data correlated strikingly with flowering data.

A new temperature summation method, based not on means but on the daily maximum and minimum and on the assumption of a linear growth curve, was designed to reflect the approximate duration of different temperature levels during the diurnal regime. The method excels use of the mean in summation only for days when rising or falling temperature crosses the threshold temperature level for the plant process or processes being studied. Such days occur frequently in the spring months.

For each of 24 species, heat sums obtained by the duration-summation formula for various presumptive thresholds and time periods were analyzed by punch-card machines for standard deviation and coefficient of variation, and these values plotted. The curves usually revealed clearly the threshold temperature for flowering (within 5° F) and the time period of spring preflowering activity (within 10 days). From these values and the mean flowering date, the requisite heat sum for flowering was found for each species.

Temperature thresholds, which are meteorological rather than physiological ones, ranged from 40° through 50° F, averaged 45°. Growth periods ranged from 20 through 50 days, and heat sums ranged from 2,034 degree-hours for an early species to 8,533 degree-hours for the next to the latest considered. In general, there is an association between long time period, high threshold, and late flowering date, and the converse.

It is concluded that a sufficiently close parallelism exists between the official meteorological records and temperatures actually influencing the plant for such records to be ecologically useful when interpreted by a suitable method.

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CERTAIN ASPECTS OF CLIMATE AS RELATED TO THE DISTRIBUTION OF LOBLOLLY PINE

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Introduction

It is generally acknowledged that the geographic distribution of plant species is restricted, to some extent at least, by the physiological responses of the plants to various aspects of climate. A number of attempts have been made to relate vegetational zones to those of climatic environment, and, although limited in scope and applicability, the results of such studies have indicated general relationships between plant formations and climate (Merriam 1894, Transeau 1905, Livingston and Shreve 1921, Mayr 1925, Huffaker 1942).

The most comprehensive studies of distribution of forest tree species in the United States have been conducted in the West, particularly in the Rocky Mountain region. Here great variations in elevation result in a zonation of vegetation, accentuating the apparent control of climate. The distribution of a number of tree species native to that region has been found to be closely correlated with temperature and moisture conditions (Shreve 1915, 1917, Bates 1924, Larsen 1930, Baker and Korstian 1931, Pearson 1931, Daubenmire 1943, and others).

Loblolly pine (*Pinus taeda* L.) is an economically important subclimax constituent of the coniferous forest of southeastern United States and, with the exception of shortleaf pine (*Pinus echinata* Mill.), has the widest distribution of all the southern pines. The present natural range of the species extends from southern New Jersey south through the Atlantic Coastal Plain and the lower Piedmont to central Florida, west to eastern Texas and southeastern Oklahoma, and north from the Gulf Coast into southern Arkansas and southern Tennessee. There is little quantitative information available concerning either the climate characterizing the loblolly pine region as a whole or the possible relations of this climate to the natural distribution of the species.

The studies of Wakeley (1944), Minckler (1950), Cummings (1952), and others indicate that, even within its natural range, loblolly pine is rather sensitive to climatic influence. The species has been planted north of its natural range with varying degrees of success (Huckenpahler 1950, Parker 1950, 1955, Shoulders 1952, Allen 1953, Minckler 1953, Wiesehuegel 1955). Some of the plantings which now appear to be successful are either too small in area or too young to permit conclusions as to their future.

It was the purpose of this study to determine which climatic factors, if any, appear to be related to the present natural distribution of loblolly pine and to test the applicability of the discriminant function as a statistical method for use in studies of this type.

The writer wishes to express his appreciation to Professors C. F. Korstian and F. X. Schumacher, of the Duke University School of Forestry, for counsel given during the course of this study. Grateful acknowledgment is due the staff of the National Weather Records Center, Asheville, North Carolina, for the many courtesies extended in making available climatological records. The writer is also indebted to the many volunteer weather observers without whose records this study would not have been possible.

Sincere appreciation is expressed to the Southeastern Forest Experiment Station for financial assistance on the project through a grant-in-aid. Thanks are especially due Dr. Carl E. Ostrom, of that station, for his interest and cooperation. Special acknowledgment is due Dorothy B. Hocker whose assistance was constant throughout all phases of the study.

Procedure and Methods

Since the results of this study would be considerably influenced by the position of the lines defining the natural distribution of the species, it was necessary to determine these limits as accurately as possible before proceeding with the study. None of the available maps of the distribution of loblolly pine was adequate for the needs of this study. Therefore, a new map was produced by drawing upon information from several sources (Fig. 2). A map prepared by the Southern Forest Tree Improvement Committee (1952) was used as a guide since, for the portion of the range shown, it was the most detailed and most recent one available. This map did not include the portions of the range within Florida, Oklahoma, and Texas. The southern boundary in Florida, as shown in Figure 2, is that defined on an unpublished map provided by the U. S. Forest Service. The geographic limits of the species within the states of Oklahoma and Texas were determined from information supplied by the Oklahoma Planning and Resources Board and the Texas Forest Service in personal correspondence. Limitations imposed in reduction of the map for publication have necessitated the omission of the detail of county boundaries included in the original map.

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Selection of the climatic variables

Selection of the climatic variables to be included in this study was necessarily governed by two basic considerations: (1) the physiological importance of the climatic factor as related to establishment and growth of plants and (2) availability of data for the climatic factor. Following consultation with climatologists of the United States Weather Bureau, it was decided that any factor could be adequately represented by a record of a minimum of 25 years within a given 30-year period. The use of records all made within a given 30-year period would, it was believed, take into account any short-term climatic trends and would, at the same time, insure that there was a true basis for comparison of data for all climatological stations. The 30-year period designated was that of 1921 through 1950.

The most complete long-term records are those for temperature and precipitation. These climatic factors are measured at all first-order as well as at a majority of older cooperating climatological stations maintained by the U. S. Weather Bureau. The selection of the variables to be used was restricted, therefore, to certain expressions of these two major climatic factors. The failure to consider such factors as evaporation, frequency of glaze storms, and relative humidity is the result of the incompleteness of such records rather than failure to recognize their possible importance. The exploratory nature of this study, as well as time and resource limitations, made it necessary to forego such possible refinements as physiological temperature indices and precipitation-evaporation ratios.

The following climatic measurements were selected to serve as a basis for the present study.

1. Average monthly temperature.—This was taken as a measure of temperature intensity which is important for the influence it has not only upon plant activity but also upon the effectiveness of other environmental conditions.

2. Average maximum and average minimum monthly temperatures.—The average monthly temperature reflects these two values as temperature intensities.[2] The difference between them provides an indication of temperature range which is an additional criterion for comparison of various locations. The range derived from maximum and minimum temperature averages was used in this study.

3. Average monthly precipitation.—Precipitation, which includes both rain and snow, was taken as a measure of the potential supply of moisture. Direct determination of the moisture content of the soil affords a more accurate index of the actual amount of water available to plants; in lieu of such measures, however, the amount of precipitation was used. The precipitation data are given in terms of inches of depth since this is the method employed by the U.S. Weather Bureau, the source of the original values.

4. Average number of days per month with precipitation of 0.01 inch or more.—In a consideration of precipitation not only the total amount but also the intensity and frequency must be taken into account. Although the total precipitation may appear to be adequate for sustaining plant growth, if it comes at frequent intervals and in such small amounts as 0.01 inch, its effect may be slight. The same amount of precipitation occurring at less frequent intervals and, hence, in larger amounts may benefit forest growth considerably. The distribution of the precipitation may be of greater importance than the total amount, particularly at certain periods of the year and at critical stages of plant growth.

5. Average number of days per month with precipitation of 0.50 inch or more.—Although the many factors which ultimately determine the amount of moisture available to plants cannot be treated in this study, some allowance can be made by considering distribution and intensity of precipitation. Precipitation of a half-inch or more is used here as an indication of effective precipitation. The amount of rain intercepted by trees is one of the factors determining precipitation effectiveness, and interception has been found to vary with intensity of rainfall. Hoover (1953) found that in a young loblolly pine stand rainfall of 0.01 inch was entirely intercepted, whereas only 12 per cent of the rain in a half-inch rainfall was intercepted by the trees. Horton (1919), Mitchell (1930), and Wood (1937) have also found a similar decrease in interception with an increase in intensity of rainfall. Although loss by interception is not the only factor to be considered, these studies indicate that a record of precipitation of intensities of a half-inch or greater is, at least in some measure, indicative of effective precipitation.

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[2] $\text{Average monthly temperature} = \frac{\text{Average maximum} + \text{Average minimum}}{2}$

6. *Dates of the last frost in the spring and the first frost in autumn.*—From these dates the number of days in the frostless season was derived. The length of the frostless season was used in this study as an approximation of the length of the growing season or period of physiological activity of plants.

Selection of climatological stations

In order to establish a basis for statistical evaluation, a minimum of 200 climatological stations were to be selected, 100 to represent the zone of natural distribution of the species and at least an equal number to represent the area outside the zone. Those stations from outside the zone were to be located within an area adjacent to the pine belt and not exceeding the approximate width of this belt at any given point. An attempt was made to obtain uniform distribution of the stations throughout the two areas, insofar as possible. In the few instances where the distribution line cut through a county, any climatological station within the county was considered as within the range of distribution. It would seem that the Mississippi bottomlands south of the northern loblolly pine limit are under the influence of the same general climate as those areas bordering them to the east and west where loblolly pine occurs. Only isolated occurrence of the species in these bottomlands is, in all probability, the result of some factor other than climate. Therefore, in the selecting of climatological stations this area was considered as within the natural range of loblolly pine.

The 220 stations initially selected were reported in recent Weather Bureau publications as having records for both precipitation and temperature covering a period of at least 30 years. Complete records were finally obtained for 207 stations, of which 83 are first-order climatological stations and 124 are cooperating stations.

Temperature and total monthly precipitation data for the 83 first-order stations were obtained from published "normals" calculated for the period 1921 through 1950 (U. S. Weather Bureau 1953). All basic data for cooperating stations and frost and precipitation frequency data for all first-order stations were obtained from U. S. Weather Bureau monthly and annual summaries published during the period 1921 through 1950. These data, with the exception of frost occurrence, were recorded for each month for which the data were available within the 30-year period. In instances where at least a 25-year record (1921-1950) could not be obtained for any factor from published climatological summaries, the station observer's original records[3] were consulted and the record thus completed. From these basic data average monthly values for each factor were calculated; average annual values were determined from the monthly averages. The summarized data for all climatological stations included in this study have been published by the Southeastern Forest Experiment Station (Hocker 1955).

In preparing the data for statistical analysis, all data except those for the frost-free period were reduced to seasonal values. Seasonal averages, in this study, are averages for the 3 months of the 4 meteorological seasons. The meteorological winter includes the months of December, January, and February; spring, March through May; summer, June through August; and autumn, September through November (Kincer 1941). Since the sum of the averages for the months within a season was divided by 3 to obtain the seasonal average, this value, as used here, is, in fact, the value for an average month within the given season. The data were entered into the statistical analysis in this form.

STATISTICAL ANALYSIS AND RESULTS

Possible correlation among the climatic factors involved in this study precluded treatment of any of them as entirely independent. A statistical method which would take into account any interrelationships between factors was required. In the discriminant function, introduced by Fisher (1936, 1948), the factors may or may not be correlated; the technique utilizes the procedural methods of multiple regression analysis and yields an equation in terms of those factors which give the maximum difference between groups relative to the differences within groups (Cox and Martin 1937). Hence, the resulting equation, or discriminant function, when applied as a means of differentiating between two groups or in classifying individuals as to group will give the smallest possible frequency of misclassification (Mather 1947). The method appeared to be appropriate to the purposes and requirements of this study and was, therefore, used in the statistical analysis.

To obtain the discriminant function, it was first necessary to establish a linear equation of the form

$$Y = a + b_1(x_1 - \bar{x}_1) + b_2(x_2 - \bar{x}_2) \ldots + b_n(x_n - \bar{x}_n)$$

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[3] On file at the National Weather Records Center, Asheville, North Carolina.

where (Y) is the calculated discriminant and (x) values are values for the several climatic factors.

The unknown coefficients b_1, b_2, b_n were solved for by the method of least squares. Each station within the natural range of loblolly pine was assigned a (y) value of plus one (+ 1) and those outside the range minus one (— 1) (Mather 1947).

Variables x_1 through x_{21} in the analysis are the following:

x_1 = Average monthly temperature, winter, in degrees F.
x_2 = Average monthly temperature, spring, in degrees F.
x_3 = Average monthly temperature, summer, degrees F.
x_4 = Average monthly temperature, autumn, in degrees F.
x_5 = Average monthly range of temperatures, winter, in degrees F.
x_6 = Average monthly range of temperatures, spring, in degrees F.
x_7 = Average monthly range of temperatures, summer, in degrees F.
x_8 = Average monthly range of temperatures, autumn, in degrees F.
x_9 = Average monthly frequency of precipitation $\geqq$ 0.01″, winter, in days.
x_{10} = Average monthly frequency of precipitation $\geqq$ 0.01″, spring, in days.
x_{11} = Average monthly frequency of precipitation $\geqq$ 0.01″, summer, in days.
x_{12} = Average monthly frequency of precipitation $\geqq$ 0.01″, autumn, in days.
x_{13} = Average monthly frequency of precipitation $\geqq$ 0.50″, winter, in days.
x_{14} = Average monthly frequency of precipitation $\geqq$ 0.50″, spring, in days.
x_{15} = Average monthly frequency of precipitation $\geqq$ 0.50″, summer, in days.
x_{16} = Average monthly frequency of precipitation $\geqq$ 0.50″, autumn, in days.
x_{17} = Average monthly precipitation, winter, in inches.
x_{18} = Average monthly precipitation, spring, in inches.
x_{19} = Average monthly precipitation, summer, in inches.
x_{20} = Average monthly precipitation, autumn, in inches.
x_{21} = Average length of the frost-free period, in days.

In completing the forward solution, the normal equations were rearranged before each reduction, and the variable making the greatest contribution to the regression sum of squares was removed first from each set of normal equations. Application of the F test showed 12 variables to be significant. The average values for the 12 significant variables are included in Table I.

TABLE I. Average seasonal values for the significant variables

Variable	SEASONAL AVERAGE*		In - out
	Within	Outside	
Average monthly temperature, winter	48.25°F	42.05°F	+6.17
Average monthly temperature, spring	63.17°F	59.30°F	+3.87
Average monthly temperature, summer	79.47°F	77.79°F	+1.68
Average range of temperatures, spring	22.75°F	22.56°F	+0.19
Average range of temperatures, summer	21.08°F	22.21°F	−1.13
Average range of temperatures, autumn	22.58°F	22.78°F	−0.20
Average monthly precipitation, spring	4.34 in.	4.05 in.	+0.29
Number days precipitation $\geqq$0.01″, winter	9.28	8.82	+0.46
Number days precipitation $\geqq$0.01″, summer	10.50	9.01	+1.49
Number days precipitation $\geqq$0.01″, autumn	6.96	7.54	−0.58
Number days precipitation $\geqq$0.50″, winter	2.93	2.10	+0.83
Number days precipitation $\geqq$0.50″, summer	3.17	2.64	+0.53

*Based upon data for 102 climatological stations within the range and 105 climatological stations outside the range of loblolly pine.

When the forward solution had been completed, a back solution was calculated to solve for the regression coefficients of the 12 significant variables. The resulting discriminant function is

$$Y = -0.0145 + 0.1986\ (x_1 - 45.09) - 0.3711\ (x_2 - 61.21) + 0.2779\ (x_3 - 78.62) + 0.2105\ (x_6 - 22.66) - 0.1296\ (x_7 - 21.60) - 0.0890\ (x_8 - 22.68) + 0.1254\ (x_9 - 9.05) + 0.1028\ (x_{11} - 9.74) - 0.3484\ (x_{12} - 7.26) + 0.4218\ (x_{13} - 2.52) + 0.1182\ (x_{15} - 2.90) - 0.0111\ (x_{18} - 41.93) \qquad (1)$$

When the appropriate mean values from Table I were substituted into equation (1) the following mean discriminants for the two regions under consideration resulted:

Within the natural range = + 0.6277 ± 0.0617
Outside the natural range = — 0.6282 ± 0.0609

or a discrimination on the average of 1.2559 ± 0.0867, a value more than 14 times its standard error.

Since the number of climatological stations within the range (102) was not equal to the number of stations outside the range (105), it was necessary to adjust (a) in equation (1) so that the calculated mean discriminants for the two regions would be values equidistant from zero. Adjustment was achieved by adding one half the difference between the two previously calculated mean discriminants to (a), changing (a) in equation (1) from -0.0145 to -0.0117. Simplifying equation (1) by removing the general means, decoding, and recalculating (a) results in the following equation:

$$Y = -8.5992 + 0.1986 (x_1) - 0.3711 (x_2) + 0.2779 (x_3) + 0.2105 (x_6) - 0.1296 (x_7) - 0.0890 (x_8) + 0.2154 (x_9) + 0.1028 (x_{11}) - 0.3484 (x_{12}) + 0.4218 (x_{13}) + 0.1182 (x_{15}) - 0.1109 (x_{18}) \qquad (2)$$

Equation (2) will yield a discriminant value indicating a climate similar to (plus) or dissimilar to (minus) that of the region of natural distribution of loblolly pine.

In using regression formulae such as equation (2), one should have some knowledge of the degree of accuracy which can be expected. In the case of the discriminant function this estimated degree of precision is referred to as the probability of misclassification. To determine the probability of misclassification for this study, it was necessary first to calculate a normal deviate. This is accomplished by dividing one half the difference between the two mean discriminants by the standard deviation of a single observation; that is

$$\text{Normal deviate} = \frac{\tfrac{1}{2}\,[0.6277 - (-0.6282)]}{\sqrt{0.389715}} = 1.006$$

According to the table of normal deviates (Pearson 1930), a deviate of 1.006 will encompass 84.27 per cent of the area under the normal curve, measured from one extreme. The remaining 15.73 per cent of the area is the region of probable misclassification. Hence, it can be expected that in using formula (2), misclassification will occur in approximately 16 of 100 applications. The chances, then, of correctly classifying any randomly selected climatological station in this study are about 5 out of 6.

By substituting the average seasonal values for each climatological station into equation (2), a calculated discriminant value (Y) was obtained for each station. The discriminant values for the stations within each of the two regions are plotted in the form of frequency diagrams in Figure 1. It can be seen in these diagrams that the application of equation (2) resulted in the misclassification of 11 stations located within the natural range of loblolly pine and 13 stations located in the region outside the natural range. Actual misclassification of stations was, therefore, somewhat lower than would be expected.

The calculated discriminant values for the 207 climatological stations have been plotted on Figure 2. It will be recalled that a calculated discriminant preceded by a plus sign denotes a classification of climate similar to that within the region of natural distribution of loblolly pine, while a discriminant value preceded by a minus denotes climate dissimilar to that of the loblolly pine region.

The two regions under consideration may be separated by a line which follows the position of the 0.00 discriminant values. This line is shown in Figure 2 and will henceforth be referred to as the calculated climatic limits of distribution of the species. This line follows rather closely the natural distribution limits. In instances where the calculated line falls inside the natural range, it is possible that the species occurs naturally beyond the calculated climatic limits as a result of modification of the local climate by edaphic and/or topographic conditions. On the other hand, where the calculated limit extends beyond the natural limit, it may be that, although the climate appears to be favorable for the establishment and growth of loblolly pine, soil conditions and/or competition from other more tolerant species prevents establishment of the species.

Figure 2 further illustrates possible climatic subdivisions within each of the two major regions. The lines drawn on the map are relative to the standard deviation of a single observation for this study and are based upon the 25 per cent and 50 per cent population limits for a normal distribution.[4] Encompassed, then, within the 25 per cent limits are those discriminant values between ± 0.43 and ± 0.83. Those lines positioned relative to the 50 per cent population limits include those discriminants of values ± 0.21 through ± 1.15. The result is the defining of 5 areas within each of the major regions; that is, 0.00 to ± 0.21; ± 0.21 to ± 0.43; ± 0.43 to ± 0.83; ± 0.83 to ± 1.15; and beyond ± 1.15. It is not to be implied that the separate portions are zones of equal climate. Such division does, however, provide a basis for comparison of areas of relatively narrow range of climate with reference to the variables found to be significant in this study.

The magnitude of the positive or negative discriminant value should indicate the relative favorableness of the climate for the growth of the species. Thus, while a discriminant of + 1.15 would indicate a very suitable climate, a discrim-

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[4] Example: $\overline{Y} \pm$ Standard deviation ($t_{0.25}$).

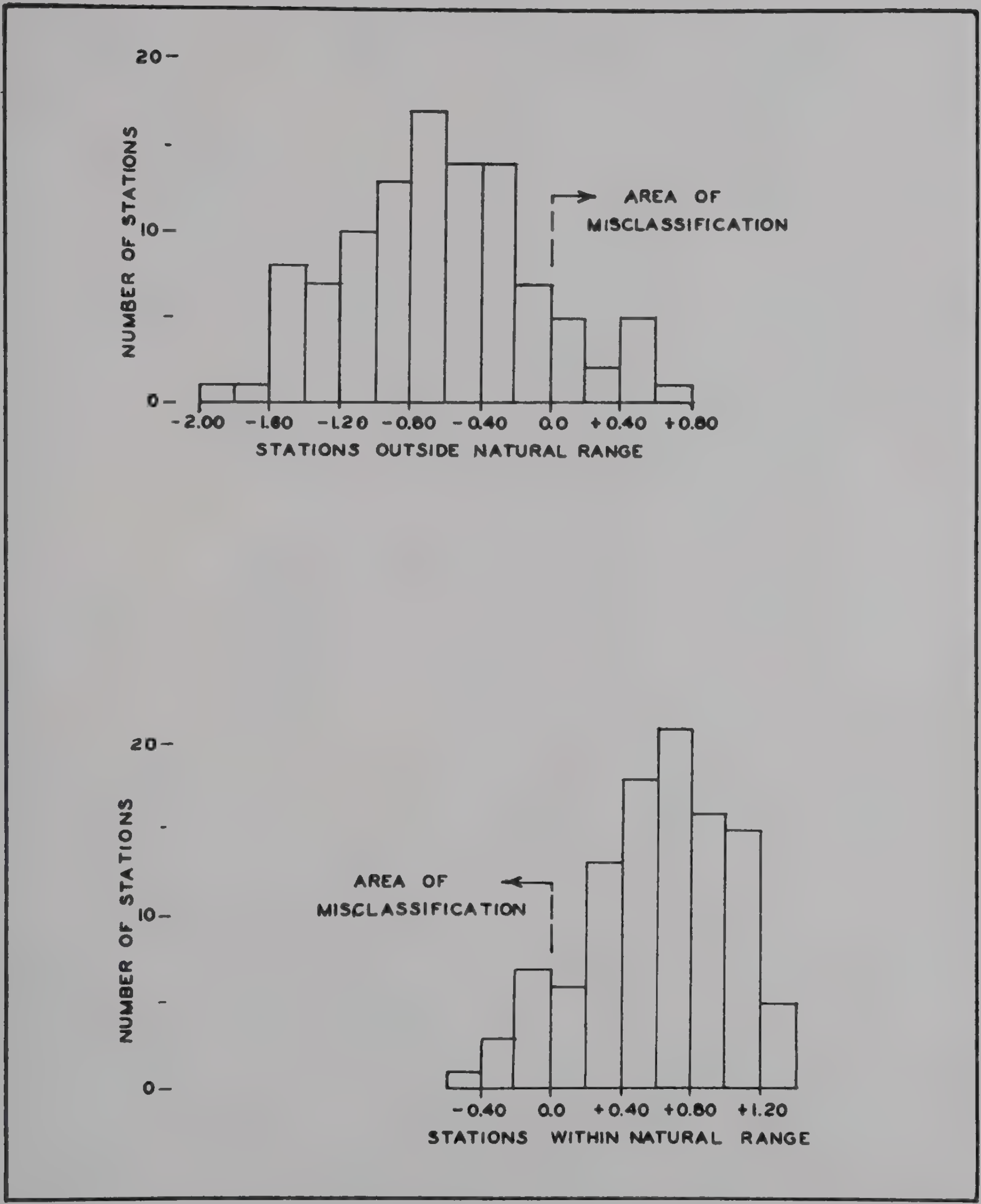

FIG. 1. Frequency diagrams of the 207 climatological stations on the basis of calculated discriminant value.

inant of — 1.15 might indicate a very unsuitable climate. A similar measure of suitability of climate may be applicable to the zones within the regions, those zones of higher positive discriminant value being better suited climatically to the species than those zones of lower positive discriminant values. The area in the Gulf Coastal Region from western Mississippi eastward is one of generally high discriminant values (Fig. 2). It is interesting to note that the results of studies by Cox (1953) and Zahner (1953) indicate that, for well-drained sites, this area is one of rela-

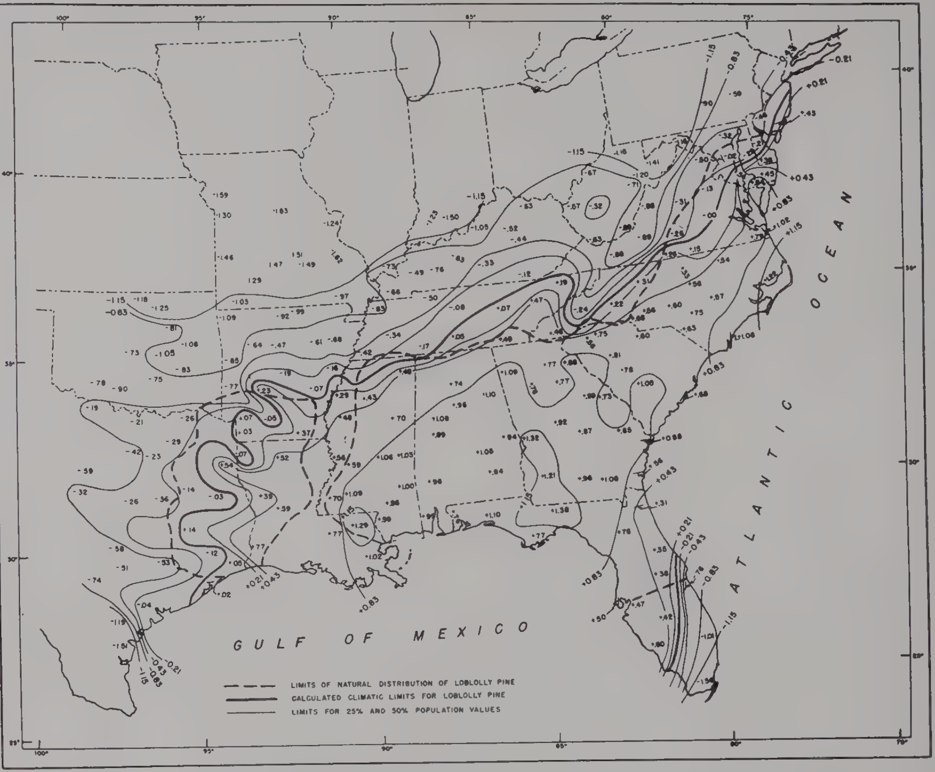
GULF OF MEXICO
ATLANTIC OCEAN
LIMITS OF NATURAL DISTRIBUTION OF LOBLOLLY PINE
CALCULATED CLIMATIC LIMITS FOR LOBLOLLY PINE
LIMITS FOR 25% AND 50% POPULATION VALUES
100°
95°
90°
85°
80°
75°
70°
40°
35°
30°
25°

FIG. 2. Map showing the calculated discriminant values for the 207 climatological stations, the natural distribution limits and calculated climatic limits of loblolly pine, and climatic subdivisions of the two regions based upon discriminant values for 25 per cent and 50 per cent of the population.

tively high site index for loblolly pine as compared with well-drained sites in other areas of the Gulf and Atlantic Coastal Plains.

DISCUSSION

The results of this study indicate that there are real differences between the climate within the loblolly pine region and that outside the natural range of the species. Although certain inferences seem justified, only an accumulation of more precise knowledge of the physiological requirements of the species will tell whether or not these differences are actually great enough to contribute to climatic control of the species.

The seasonal averages for the 12 significant factors are included in Table I. The seasonal averages for temperature and for amount of precipitation are shown graphically in Figure 3. The results of this study indicate that frequency and intensity of precipitation are better measures of differences between the two regions than is the amount of precipitation. These factors are correlated, however, and the average amount of precipitation is more commonly used in diagrams of this type. Combined with temperature, it illustrates the general patterns for the two areas and the differences between them.

During the winter season, the loblolly pine region has not only a greater total number of days with precipitation and a greater frequency of effective precipitation but also an average temperature somewhat higher than that of the region outside the range of the species. These temperature and moisture conditions may represent a real influence on the distribution of loblolly pine. Following the summer growing season and the relatively dry autumn, soil moisture content in both regions would be at its lowest at the beginning of the winter season. The greater frequency and intensity of precipitation within the loblolly pine region would result, it seems, in replenishing the soil moisture supply sooner and with greater certainty than would be the case in the region outside the range. Since temperature conditions are

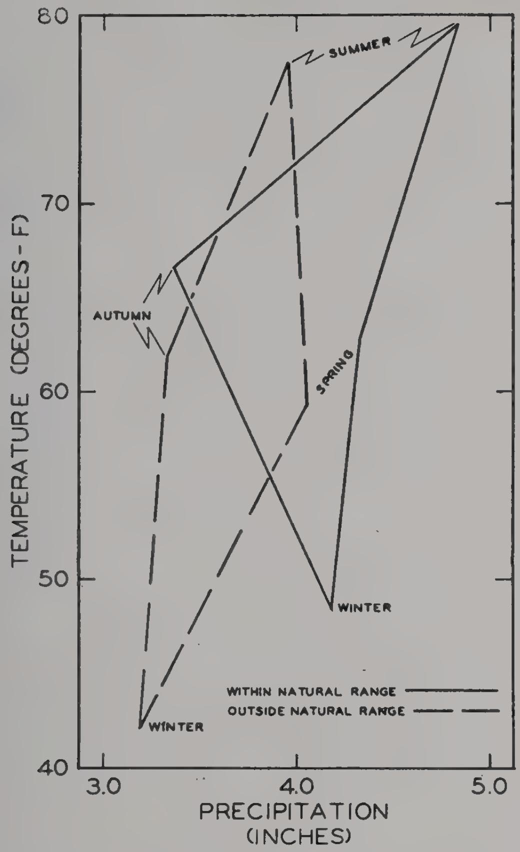

FIG. 3. Climographs showing average seasonal values of temperature and amount of precipitation for the region within the range of loblolly pine and the region outside its range.

favorable, the chance that this moisture would be available to the trees appears good. Segregation of the influence of temperature and moisture conditions during this season is difficult, particularly when considering the northern limits of the species. If adequate moisture is not available as a result of either low supply or low soil temperature, damage to trees may result. That the rate of water absorption by loblolly pine is considerably decreased with a decrease in temperature has been demonstrated by Kramer (1942) and Kozlowski (1943). A combination of temperature and moisture conditions during the winter season, then, may contribute to defining the northern limits of the species. It appears likely that the far western and southern limits would be influenced more by the frequency and intensity of precipitation during this season.

In the spring, the differences in temperature range and amount of precipitation for the two regions are so small that it is difficult to visualize these factors as influencing the distribution of the species. It should be noted that the very small difference between the amounts of precipitation for the two regions during this season, as compared with the differences for winter and summer, is due to a definite rise in the amount of precipitation outside the range rather than any decided decrease in the amount of precipitation within the range (Fig. 3).

The average spring temperature within the loblolly pine region is 3.9°F higher than that for the region outside the range. This difference is small; however, the use of average seasonal temperatures as a basis for comparison may obscure monthly differences which might be of importance to flowering.

The greatest differences between the two regions during the summer season are those for the number of days with precipitation of 0.01 inch or more and for the number of days with precipitation of 0.50 inch or more. The greater frequency and intensity of precipitation within the range of loblolly pine during this season would tend to give the region the more favorable moisture conditions and to offset more effectively losses of water resulting from evaporation and transpiration. The differences for average temperature and for range of temperature during the summer, although statistically significant, are so small that it seems unlikely that these factors would have any real effect in limiting the distribution of the species.

In autumn, as in spring, the two regions appear to be climatically similar. The temperature range, as represented by the difference between maximum and minimum temperatures, and the frequency of precipitation of 0.01 inch or more are only slightly greater outside the loblolly pine region. It seems questionable, then, that these factors would have any marked influence upon the natural distribution of the species. Comparison of the 4 seasonal averages for the amount of precipitation within the range of loblolly pine shows that autumn precipitation (3.36 inches) is decidedly lower than that for either summer (4.85 inches), winter (4.18 inches), or spring (4.34 inches). This decided decrease in total precipitation during autumn is not evident in the data for the region outside the natural range. It may be that relatively dry conditions are necessary for ripening and subsequent dispersal of seed. More quantitative information regarding the moisture requirements of the species would aid interpretation of the possible importance of this relative decrease in precipitation.

The absence of any significant regional differences attributable to the length of the frost-free period is surprising, particularly in view of the importance generally attached to this factor. The data show an average frost-free period of 239 days for the loblolly pine region and 217 days for the adjacent region. The difference between the two averages (22 days) is fairly large. However, in the statistical analysis, the sum of squares for the frost-free period was decidedly reduced when the effect of average winter temperature was removed. It appears, then, that there was a high degree of correlation between these two factors and that the effect of length of the frost-free period was absorbed by winter temperature. The difference in average autumn temperature was also absorbed by the average winter temperature. The difference between the two regions in average autumn temperature was 3.5°F, a difference almost as large as that for average spring temperature (3.9°F) which was statistically significant. Removal of the effect of average winter temperature, however, rendered the autumn temperature difference insignificant.

In general, somewhat higher average temperatures and greater precipitation characterize the climate of the loblolly pine region as compared with that of the region outside the natural range of the species. The greatest differences between the two regions are those for the winter and summer seasons. Frequency and intensity of precipitation, particularly during these two seasons, may be of importance in limiting the distribution of the species. The effect of winter temperature, it is believed, would be an indirect one acting through its influence upon the availability of soil moisture. It should be remembered, however, that there is strong correlation among the several climatic variables and that apparent statistical significance of any given variable depends, in part, upon the order in which the variables are removed in the reduction of the normal equations. Therefore, caution must be exercised in drawing conclusions as to the relative importance of a variable. Further, no allowance can be made for local features of the environment which might tend to modify the effect of any given climatic factor.

In assembling the data for statistical analysis, it was observed that along the northern limits of loblolly pine the differences in temperature between the two regions appeared to be more pronounced than precipitation differences, while along the western boundary precipitation differences appeared greater. Any such tendencies would be obscured in considering average values for entire regions. If each of the two regions was divided into two or more comparable portions such that the northern extension of the range might be considered separately from the western extension, it might be possible to determine whether or not temperature is more important along the northern limits and precipitation along the western limits.

The error of probable misclassification in this study is sufficiently small, considering the diversity of the data, to indicate that the discriminant function can be used successfully as a statistical method for segregating those climatic factors which best differentiate between two regions. However, limitations will be imposed upon any statistical method and the interpretation of the results with regard to climatic control of the distribution of loblolly pine until such time as there are sufficient data to employ expressions of the interaction between climatic factors. Also, there is a need for more information regarding the physiological response of loblolly pine to varying intensities of precipitation and temperature, especially as they are related to flowering and to seed production and dispersal.

The discriminant values calculated in this study indicate that there are only 3 areas in the region adjacent to the present natural range of loblolly pine where the climate is similar to that within the natural range. These areas are (1) southeastern New Jersey, (2) the Tennessee Valley north to Knoxville, and (3) southwestern Florida (Fig. 2). If soil and other site factors are favorable, it is possible, then, that the range of the species could be extended successfully into these areas. It may also be that the zone of generally low negative discriminant values bordering the northern limits of distribution may represent a transition zone into which some extension of the species may be possible. Further, it is possible that modification of the climate by edaphic and topographic conditions may permit some localized extension of the range into the region of negative discriminants. However, considering climate alone, no appreciable northward extension of the limits of the species would seem feasible.

Early favorable reports have been made of some plantings of the species in Tennessee, Kentucky, and Illinois in the region of negative discriminant values. These plantings, reported by Huckenpahler (1950), Allen (1953), and Minckler (1953), respectively, are not yet old enough to permit conclusions as to the adaptability of the species to these locations where the climate is apparently unlike that within the natural range of loblolly pine.

The discriminant equation derived in this study can be used in determining whether or not the climate of a location in another section of the country might be favorable to growth of loblolly pine. Such an application has been made using data for Placerville, California. An experimental planting of loblolly pine there is reported to be producing viable seed.[5] Substitution of data for this station into equation (2) resulted in a calculated discriminant value of + 2.02. Although the precipitation pattern there is somewhat different from that within the loblolly pine region, apparently considerable general similarity exists between the two climates as represented by those variables found to be significant in this study.

The discriminant equation resulting from this work may find further application in other types of studies of loblolly pine. It has been found that in predicting the success and in interpreting the results of experimental plantings it is often desirable to compare the climate at the seed source with that of the area in which the seed is planted. Soil-site studies for this species indicate that climatic factors are of importance to height growth even after the effect of soil factors has been taken into account (Cox 1953, Zahner 1953). The discriminant equation provides a means of comparing two or more localities with reference to those factors which appear to be correlated with the natural distribution of loblolly pine and may, therefore, be of use in other studies such as those of soil site and the geographical source of seed.

SUMMARY

A study was made of the relation between certain climatic variables and the natural distribution of loblolly pine. All basic climatological data used were obtained from records made by U. S. Weather Bureau observers during the period 1921 through 1950. There were 207 climatological stations represented in the study, 102 located within the present natural range of loblolly pine and 105 located outside the range but within an area adjacent to the loblolly pine region. To determine whether or not there is a significant climatic difference between the two regions, statistical analysis of the data was made by methods appropriate to the discriminant function.

Twelve factors were found to contribute significantly to the climatic difference between the two regions. A discriminant equation was derived in terms of these 12 factors. This equation can be applied as a means of classifying a given location with reference to the climate of the loblolly pine region. When the appropriate data for a given climatological station are substituted into the equation, a calculated positive (Y) value indicates a climate similar to that within the loblolly pine region, whereas, a negative (Y) value indicates a climate dissimilar to that within the region. Using this equation, the chances are 5 in 6 that any station from a selection of stations chosen at random will be correctly classified.

The calculated climatic limits of loblolly pine, based upon the 0.00 discriminant value, followed rather closely the natural distribution limits of the species.

Average temperature and frequency and intensity of precipitation during the winter season and frequency and intensity of precipitation during the summer season appear to be the factors which contribute most to limiting the distribution of loblolly pine. It is believed that the effect of average winter temperature would be through its influence upon the availability of soil moisture.

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PHOTOSYNTHESIS AND RESPIRATION OF THE PHYTOPLANKTON IN SANDUSKY BAY[1]

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A study of the photosynthesis and respiration of the phytoplankton in Sandusky Bay (Fig. 1) was conducted from February 2 to June 18, 1954. The Bay empties into Western Lake Erie, and the study was undertaken to supplement the investigations carried on at the F. T. Stone Laboratory on the phytoplankton of western Lake Erie (Chandler 1940, 1942, Verduin 1952).

The writer wishes to acknowledge the guidance of Dr. Jacob Verduin and of Dr. Thomas H. Langlois. The management of the Winous Point Shooting Club provided laboratory facilities.

METHODS

The method used for determination of rates of photosynthesis and respiration has been described by Verduin (1956). A series of 7 clear and 2 blackened, glass stoppered, test bottles of 140 ml capacity was used. The bottles were filled by submerging in a pailful of surface water and stoppered under water to eliminate air bubbles. They were then attached horizontally to a cord in a vertical series at 0.1 m intervals with the blackened bottles at the bottom of the series. These were suspended in the Bay with the first bottle at the surface and at such a position that the bottles received unobstructed exposure to the light.

The phytoplankton population in the water

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[1] From a Ph.D. dissertation "Photosynthesis and Respiration of the Phytoplankton in Sandusky Bay," The Ohio State University, 1954.

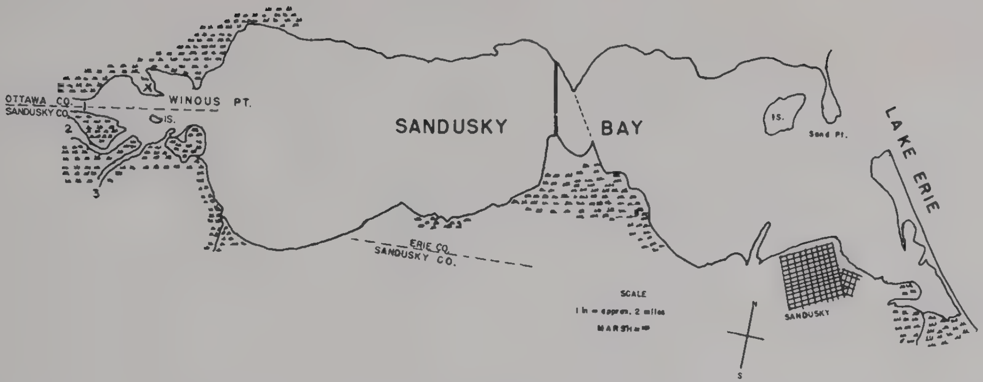

FIG. 1. A map of Sandusky Bay modified from the U. S. Lake Survey Map (1949) by the Corps of Engineers of the U. S. Army. The location of Winous Point is indicated by (x). Tributaries flowing into the Bay are (1) Muddy Creek, (2) Sandusky River, and (3) South Creek.

sample was assessed by direct count at a magnification of 100x in a Sedgwick-Rafter cell (Welch 1948), the lower limit of organismal dimensions detected by this method was about 2 microns. The organisms were measured and volumes computed; standing crops were expressed in units of $10^{10}\mu^3$ of plant volume. Temperature, initial pH, dissolved oxygen, free carbon dioxide, phenolphthalein and methyl orange alkalinities were determined for each sample (Standard methods for the examination of water and sewage. 8th ed.).

After 6 hours' exposure (9 A.M. to 3 P.M.), the bottles were removed from the Bay, submerged in a pail of water to prevent change of temperature, and carried to the laboratory where the pH was recorded for each bottle. The pH change in the open water during the test period was also measured to estimate apparent photosynthesis under completely natural conditions.

Light intensity at the surface of the water and at 0.1 m intervals was measured at 10 A.M. and at 2 P.M. by means of a Weston photronic cell, Model 856RR, enclosed in a water-tight case. This instrument yielded a current of 20 milliamperes at the surface in clear weather, and could be read accurately to 1 microampere.

A parallel study of photosynthesis and respiration was made by measuring oxygen change in three 300 ml bottles, one of which was light-proof. One clear botttle was held horizontally at the surface and the second at 0.2 m. All dissolved oxygen analyses were made by the Winkler method (Standard methods for the examination of water and sewage. 8th ed.).

The total suspensoids and ash-free dry weight of organic matter per liter were determined gravimetrically by centrifuging a liter of the sample water in a Foerst centrifuge, drying the concentrate in a constant temperature electric oven at 60°C, weighing, igniting, and reweighing (Welch 1948).

RESULTS AND DISCUSSION

Table I shows the minimum, maximum and average values of dissolved oxygen, pH, total alkalinity, depth associated with 10% of surface light intensity (the decimal reduction distance, DRD), total supensoids and ash-free dry weights.

TABLE I. Minimum, maximum and average values

	Minimum	Maximum	Average
Dissolved oxygen	5.92 ppm	14.25 ppm	10.3 ppm
pH	7.74	9.06	8.25
Total alkalinity	79.0 ppm	210.0 ppm	132.0 ppm
DRD	0.03 m.	0.92 m.	0.36 m.
*Oven-dry suspensoids	30.0 mg./L.	1128.4 mg./L,	121.7 mg./L.
*Ash-free dry weights	5.8 mg./L.	300.0 mg./L.	25.5 mg./L.

*Data for period May 3 to June 18, inclusive

Dissolved oxygen was usually near saturation, pH was similar to that of western Lake Erie (Chandler 1940), total alkalinity about 50% higher (Chandler 1940), DRD about one-tenth of that of western Lake Erie (Verduin 1952), and ash-free dry weight about 8 times higher (Andrews 1953).

The rates of total photosynthesis (micromoles CO_2 absorbed per hour per unit of plant volume) on 5 different days are plotted against light intensity (Fig. 2). The highest curve shows maxima about 2.5 times the values of the lowest curve. The points for each day present a fairly smooth curve. All the curves show some degree of inhibition at the surface, regardless of the surface light intensity. In each case, the maximum rate appears in the second bottle of the series 0.1 m be-

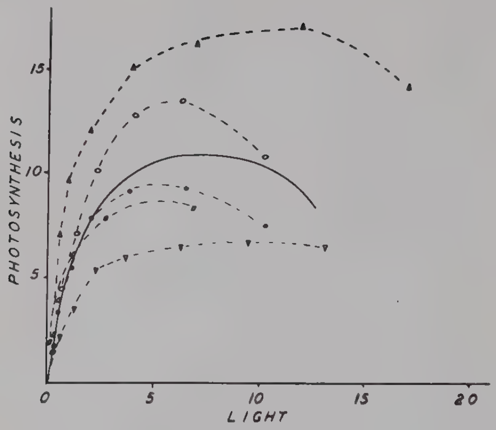

FIG. 2. Total photosynthesis (micromoles CO_2 absorbed/hour/$10^{10}\mu^3$) graphed against light (milliamps Weston photronic cell). The broken lines represent rates on 5 different days. The solid line indicates the average of the 5 days.

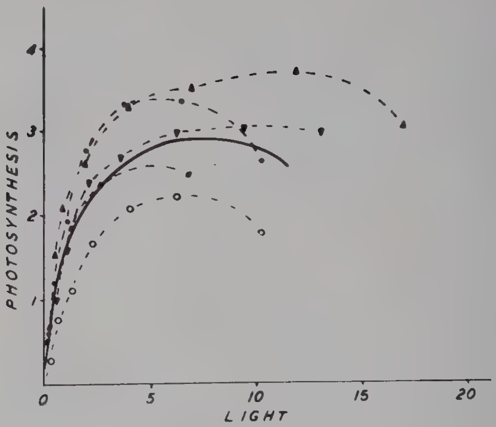

FIG. 3. Total photosynthesis (micromoles CO_2 absorbed/hour/mg. ash-free dry weight) graphed against light (milliamps Weston photronic cell). The broken lines represent rates on 5 different days. The solid line indicates the average of the 5 days.

low the surface. The rates on any single day cannot be considered a representative sample, but the mean of several days represents a more reliable estimate of average photosynthetic yield.

In Figure 3, the photosynthetic rates, based on micromoles CO_2 absorbed per mg. ash-free dry weight of suspensoids for the same 5 days as in Figure 2, are plotted against light. In this graph, similar curves appear but the spread is reduced considerably. The maximum of the highest curve being only 1.7 times that of the lowest curve. These data suggest that ash-free dry weight of suspensoids was a better index of photosynthetic capacity than was the volumetric standing crop of phytoplankton for these 5 samples.

During the period of investigation, water temperatures ranged from 0°C to 25°C (thermal stratification was not present). However, no consistent correlation between photosynthesis and temperature was observed.

Photosynthetic rates per unit of plant volume per hour were graphed against standing crop of phytoplankton per liter (Fig. 4). The mean shows a gradual downward slope over most of the graph but a sharp bend and a rapidly ascending rate appears at the population level of about 0.3 x $10^{10}\mu^3$. The data indicate an inverse ratio between photosynthetic rates and the standing crop. The rates per unit of plant volume were very high during periods of extremely low populations. It seems likely that an important phytoplankton component escaped detection at the 100-fold magnification used in counting. This component is responsible for most of the photosynthesis measured when the observed phytoplankton crops are low (Verduin 1956). When the observed standing crops were high, the yield per unit plant volume approached a value of about 8 micromoles per hour. These values are slightly higher than the values of about 5 observed in western Lake Erie using concentrated populations (Verduin 1956). The hourly photosynthetic rates per liter of water (Fig. 4) show a rough positive correlation with standing crop but considerable amounts of photosynthetic activity are observed when standing crops approach zero.

A curve similar to that of Figure 4 was obtained from the oxygen evolution data. The ratio of CO_2 consumed to O_2 evolved (CO_2/O_2) was 0.87. Photosynthetic rates per mg. ash-free dry weight of suspensoids averaged 2.4 micromoles CO_2 consumed per hour.

In Figure 5, photosynthesis (micromoles CO_2/hr/liter of water) is plotted against ash-free dry weight of suspensoids; a correlation coefficient of 0.604 was obtained which is statistically significant at the 5% level. Correlation of CO_2 consumption with phytoplankton volume was 0.388; of O_2 evolution with ash-free dry weight was 0.413; of O_2 evolution with phytoplankton volume was 0.457. These low correlations indicate that photosynthetic yields show wide variation whether related to phytoplankton volume or ash-free dry weight of suspensoids, and whether determined by measuring CO_2 change or O_2 change.

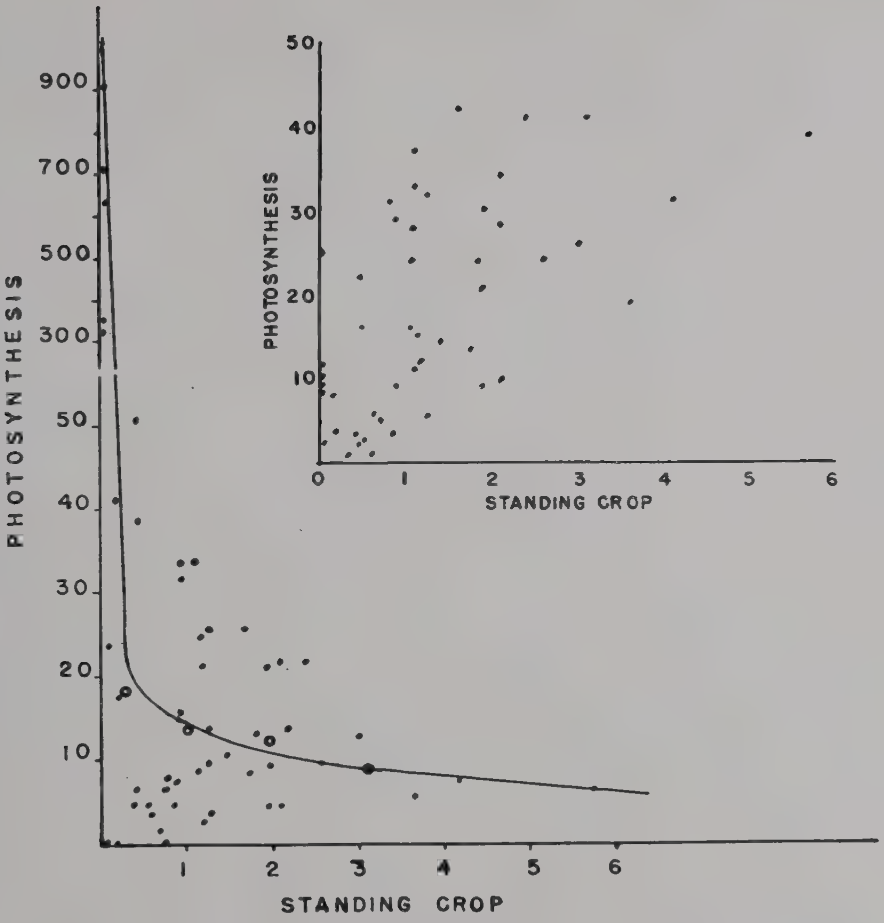

FIG. 4. Total photosynthesis per unit plant volume at optimal light (micromoles CO_2 absorbed per hour) plotted against the standing crop. Insert shows hourly photosynthesis per liter of water vs. standing crop.

The rates of apparent photosynthesis in the open water averaged 12 micromoles/hr/liter of water. The average total photosynthesis at optimal light in the experimental bottles was 17 micromoles CO_2 consumed/hr/liter, and the average apparent photosynthesis was 13. These data indicate close agreement between changes in the open water and changes in the experimental bottles, with apparent photosynthesis accounting for about three-fourths of total photosynthesis.

Although photosynthetic rates determined from CO_2 change agreed closely with those based on O_2 change, the respiration rates based on CO_2 change were several times higher than those based on O_2 change. A respiratory quotient (CO_2/O_2) computed from the data showed a value of 3.3. This high value suggests the presence of a population producing CO_2 at a rate much higher than its O_2 consumption, or that some other process causing a lowering of pH is occurring, thus obscuring the true CO_2 evolution rate.

The light absorption coefficient (Verduin 1954) was calculated from the data obtained. This coefficient varied from 0.07 to 0.15 and averaged 0.12 for the samples. This average value was very close to the average reported for Lake Erie, although the average concentration of suspensoids is 10 times greater in Sandusky Bay than in Western Lake Erie.

The distribution of phytoplankton populations in relation to decimal reduction distances is portrayed in Figure 6. Population means are plotted for each 0.1 m interval. This graph reveals a positive correlation of the standing crop with light penetration between abscissa values of 0.0-0.4, but beyond this point, the correlation between light

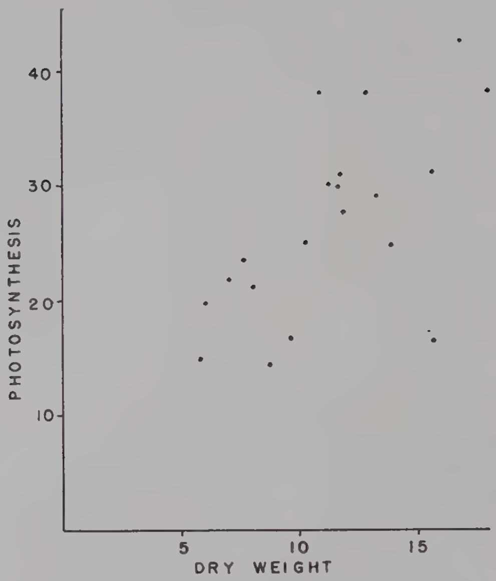

Fig. 5. Total photosynthesis (micromoles CO_2 absorbed/hour/liter) at optimal light graphed against ash-free dry weight of suspensoids in water (mg. per liter).

penetration and standing crop disappears. These data suggest that when DRD is reduced to less than one-third of the total depth, light is severely limiting and the development of the phytoplankton crop is prevented, but when the DRD is greater than one-third of the water column, factors other than light supply exert a controlling influence on the size of the standing crop. Verduin (1954) observed that when 1% of surface light penetrated to less than half of the water column in western Lake Erie, phytoplankton crops remained at low levels.

At the start of the study on February 2, the phytoplankton population was at a level of 2.54 x $10^{10}\mu^3$ per liter. Ninety three per cent of the crop consisted of *Cyclotella,* the largest component of which was identified by the author as *Cyclotella michiganiana* Skvortzow and this identification was confirmed in private communication by L. H. Tiffany. This genus was represented by 25 million cells per liter. The low crop in April, 0.007 x $10^{10}\mu^3$ per liter, comprised a mixture of diatoms with no single form predominating. The June pulse attained a crest of 5.73 x $10^{10}\mu^3$ per liter of which *Melosira varians* C. A. Agardh and *M. granulata* (Ehrenberg) Ralfs. comprised 65% of the population. The Bacillariophyceae constituted 96.7% of the February crop and 93.5% of the June crop. Thus, the species composition of the phytoplankton is in general similar to that of western Lake Erie (Chandler 1940) but *Cyclotella michiganiana* has not been reported as a major

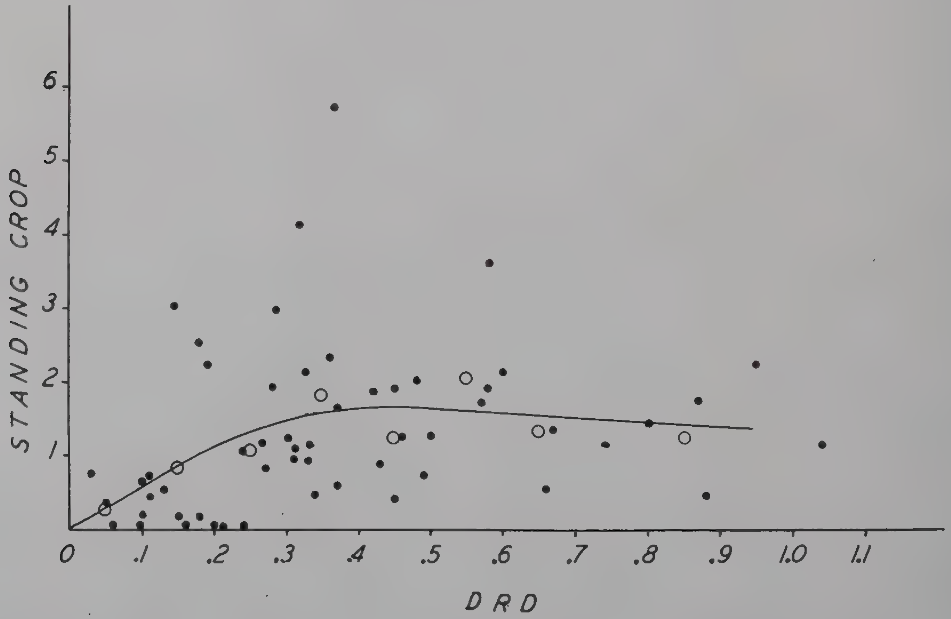

Fig. 6. Population of phytoplankton (μ^3/liter x 10^{-10}) plotted against decimal reduction distance (DRD). Means for each 0.1 m are indicated by open circles.

component in western Lake Erie, although other species of *Cyclotella* are abundant there.

The high ratio of CO_2/O_2 observed in the black bottles (respiration measurements) suggests that a significant population of "fermenters" is present; or that some acid other than H_2CO_3 is being produced by some process, biologic or otherwise. The phenomenon has not been observed before in natural waters, to my knowledge, perhaps because students of productivity have followed O_2 changes without measuring CO_2 changes at the same time. It may be that discrepancies of this sort can be observed frequently in natural aquatic environments. The phenomenon certainly warrants further investigation.

In Figure 4, the phenomenon of sharply increasing photosynthesis per $10^{10}\mu^3$ appears with low levels of standing crop and the entire curve shows an inverse relation to the phytoplankton population. For several weeks during the summer of 1953, studying samples taken from Put-in-Bay, I observed a similar pheonomenon, and experiments with Lake Erie water from which the phytoplankton had been removed by a No. 25 silk bolting cloth filter, showed average photosynthetic rates of 2.3 micromoles CO_2 removed per liter per hour. Obviously, these rates are attributable to a component of the phytoplantkon not retained by the bolting cloth filter. It may be that algae of small dimensions escape detection, but in the direct count method employed in the present study it seems unlikely that spherical algae, even as small as 2 micra in diameter, would have escaped detection if they were present in the quantities required to explain the photosynthetic rates observed when standing crops approached zero. Another possibility is that aquatic environments contain important bacterial communities (Henrici 1939) (chemosynthetic, photosynthetic, and reducers) whose metabolic activities may contribute to the inverse correlations observed in Figure 4 and to the high CO_2/O_2 ratio (fermenters, H_2S producers).

SUMMARY

A study of photosynthesis and respiration of natural communities in Sandusky Bay, on the southwest shore of Lake Erie, was made from February 2 to June 18, 1954.

Average photosynthetic rates, when phytoplankton counts were high, amounted to 8 micromoles CO_2 removed/hr/$10^{10}\mu^3$ and 2.4 micromoles/hr/mg. ash-free dry weight of suspensoids. The photosynthetic quotient (CO_2/O_2) observed had a value of 0.87. Apparent photosynthesis under completely natural conditions amounted to about 75% of total phtosynthesis as measured in clear and blackened bottles.

Relatively high photosynthetic rates at low levels of phytoplankton populations indicate the presence of important quantities of organisms that are not detected by observation under 100x magnification. A respiratory quotient (CO_2/O_2) of 3.3 was observed, suggesting CO_2 evolution considerably in excess of O_2 consumption. It is suggested that microbial components may be responsible for the high photosynthesis associated with low phytoplankton volumes and for the high value of the respiratory quotient.

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NOTES AND COMMENT

THE SOLUBILITY OF 3-BROMO-4-NITROPHENOL IN WATER AND ACETONE

The threat to the fishes in the Great Lakes, particularly lake trout, whitefish, suckers and walleyes, caused by the advent of the sea lamprey (*Petromyzon marinus*) has received a good deal of attention recently (see, for example, papers of Applegate). 3-Bromo-4-nitrophenol has shown some promise as a larvicide which is specific toward the sea lamprey (personal communication from V. C. Applegate). In order that effective introduction of this substance in streams may be achieved, some knowledge of the solubility of this compound and the variation of solubility over the range of normal stream temperatures is desirable.

The 3-bromo-4-nitrophenol used in the measurements reported here was kindly supplied by Dr. M. A. Smith and Dr. H. W. Heine of this laboratory. It had a melting point of 133-4°C. The water used as solvent was singly distilled and the acetone was N.F. grade used without further purification.

Measurements were carried out at constant temperature in a water bath thermostatically controlled to ± 0.02° C. A nearly-saturated solution of the compound in the solvent at an elevated temperature (*ca.* 40-50° C) was prepared in a ground-glass-stoppered test tube. This test tube was placed in the constant temperature bath for several hours. In the water solubility measurements the test tubes were agitated continuously by a mechanical device which turned them slowly end over end. The acetone solutions were not agitated because of their small volume. When the solution cooled to the bath temperature, the excess solute precipitated, leaving a saturated solution. A quantity of the supernatant liquid was withdrawn by pipet through a filter to prevent small crystals from entering the pipet. The liquid was quickly discharged into a weighed vessel which was closed as soon as possible to prevent evaporation of the solvent and then reweighed to determine the total weight of solute and solvent. The solvent was then evaporated by passing a slow stream of dry air over the vessel. When most of the solvent had evaporated, the residue was dried to constant weight in an oven at 110° C and the weight of the residue was determined. At least two determinations were made at each temperature.

The results of these measurements are given in Table I. If it is assumed that the heat of solution is independent of temperature over this comparatively small range, a plot of the logarithm of the solubility versus the reciprocal of the absolute temperature should give a straight line. Such a graph is shown in Figure 1.

The data indicate that the solubility of the compound in water is probably sufficient for larvicidal use in streams. Introduction into the stream can be facilitated by use of a concentrated acetone solution.

This work was carried out under the auspices of the Hammond Bay Fishery Laboratory of the U. S. Fish and Wildlife Service.

TABLE I. Solubility of 3-bromo-4-nitrophenol in Water and Acetone

Temperature, °C	Solubility in Water, g/1000 g H_2O	Solubility in Acetone, g/g acetone
30.00	....	2.62
	....	2.68
		Avg. 2.65
29.80	2.24	
	2.20	
	Avg. 2.22	
25.00	1.84	2.48
	1.76	2.59
	Avg. 1.80	Avg. 2.54
20.00	1.48	2.43
	1.45	2.42
	Avg. 1.46	Avg. 2.42
15.50	....	2.26
	....	2.32
		Avg. 2.29
10.00	0.96	
	1.00	
	Avg. 0.98	
0.00	0.67	2.08
	0.65	2.08
	0.60	Avg. 2.08
	0.60	
	Avg. 0.63	

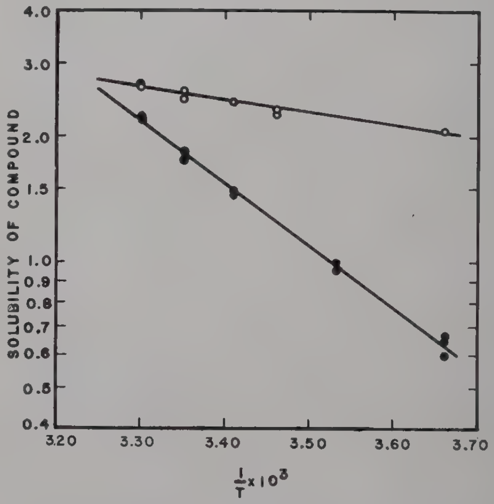

FIG. 1. Temperature dependence of solubility of 3-Bromo-4-nitrophenol. Closed circles—grams of compound per 1000 grams of water. Open circles—grams of compound per gram of acetone.

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THE SHIPWORM *TEREDO NAVALIS* IN MARYLAND COASTAL WATERS[1]

The Teredinidae, or shipworms, a family of wood-boring bivalve molluscs, cause extensive damage to waterfront structures. Scheltema and Truitt (1954) summarized the occurrence of *Bankia gouldi* Bartsch in Chesapeake Bay; however, no study of the Teredinidae has been made along the Maryland Atlantic coast, an area which supports important fisheries at Ocean City and active crab, oyster, and hard clam industries in Chincoteague Bay. Brown (1954) has reported the results from test panels submerged at Lewes, Delaware, and at Winter Quarter Shoal Lightship off Assateague Island, Virginia. A preliminary investigation of the area lying between these two points and including the Maryland portion of Chincoteague Bay is reported here.

Racks of test panels were submerged at three stations. Two were located in the northern half of Chincoteague Bay, at Rattlesnake Landing and at Snow Hill Public Landing, and one near the inlet in Ocean City harbor (Fig. 1). The test panels were installed between June 1950 and September 1953. A total of one hundred and fifty-seven 2 x 4 x 6-inch pine panels were exposed to shipworm attack. Five types of data were obtained: (1) the months during which a set of shipworms occurred, (2) the magnitude of the set for each month, (3) the magnitude of the set for each year, (4) the vertical distribution of the set, and (5) the rate of boring for each month.

Data obtained from test panels at Ocean City are shown in Figure 2. The species of shipworm was *Teredo navalis* Linné.[2] The magnitude and time of set varied considerably during the three-year period. The heaviest set occurred during 1951 with a peak in August and September; the lightest, during 1952 with peaks in July and October.

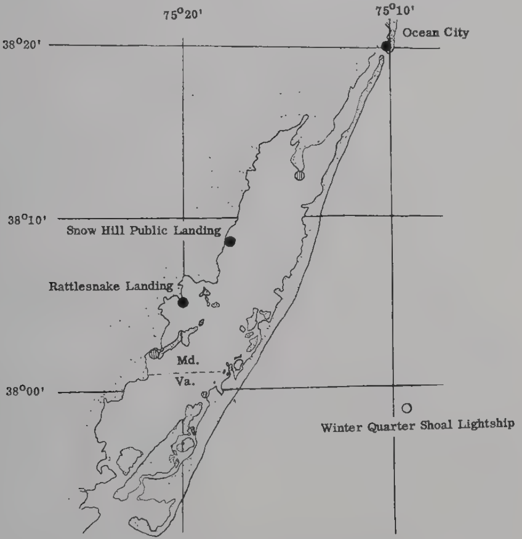

Fig. 1. Chincoteague Bay and adjacent waters. The dark circles indicate the location of test panel stations. Hatched circles indicate points from which collections of *Teredo navalis* were made by the authors during the spring of 1954. Open circle indicates test panel station reported by Brown (1954).

In Figure 3 is shown the vertical distribution of *Teredo navalis* at Ocean City during the summer of 1952. The intensity of the set was greater below mean low water and increased with depth.

The mean total burrow length and the monthly rate of boring are indicated in Figure 4. These data were obtained from a series of panels submerged in July 1950. One panel was removed each month, and the mean burrow length, the average of the ten longest burrows, was determined. The rate of boring, *i.e.* the distance bored during a month, was computed by subtracting the

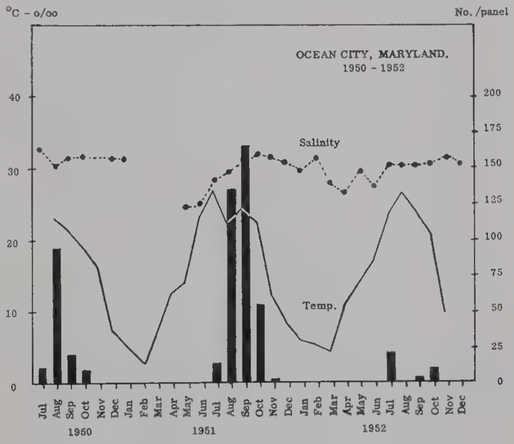

Fig. 2. Magnitude of set at mid-depth, *Teredo navalis*, by month for three seasons at Ocean City, Maryland, 1950 through 1952. Dashed line indicates salinity in parts per thousand. Solid line indicates temperature in degrees C.

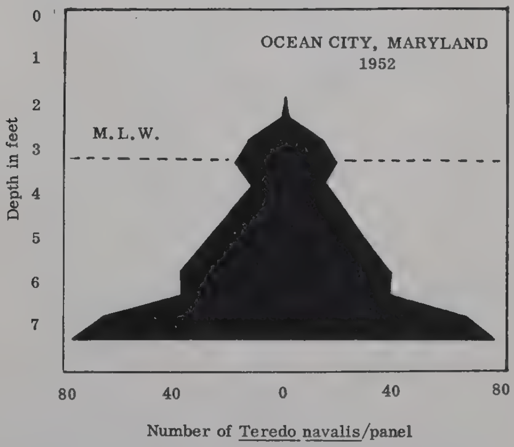

Fig. 3. Vertical distribution of set, *Teredo navalis*, during the summer of 1952 at Ocean City, Maryland. M. L. W. = mean low water.

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[1] Contribution number 103, Chesapeake Biological Laboratory, Maryland Department of Research and Education, Solomons, Maryland.

[2] Specimens have been deposited with the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

mean length of any given month from that of the previous month.

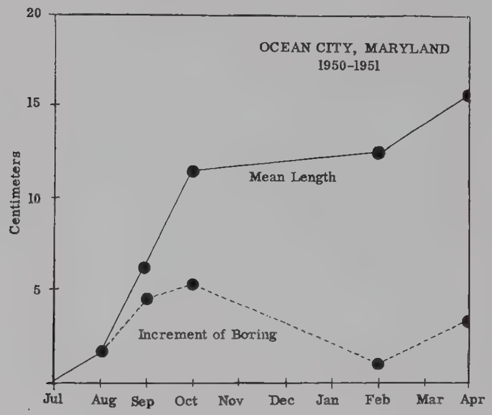

FIG. 4. Mean length of burrows and apparent rate of boring in centimeters per month of *Teredo navalis* at Ocean City, Maryland, 1950-1951. Each point on the graph represents the results from one test panel.

Figure 4 shows that most of the boring occurred during late summer and early fall and that the maximum rate was attained during the month of October. Previous work has shown that decrease in the rate of boring is attributable to overcrowding (Isham *et al.* 1951), decreased activity due to a decrease in temperature (Needler and Needler 1940), or decreased activity related to increased age of the organisms. Since our sample taken in February contained relatively few *Teredo navalis,* the decrease in boring rate in this instance was probably not caused by overcrowding. The increase in boring rate between February and April 1951 is suggestive of an increased rate of boring with increasing temperature.

Chincoteague Bay is a bar-built estuary extending along the Maryland and Virginia coast for approximately 23 nautical miles. The bay opens to the northeast through Sinepuxent Bay and Ocean City Inlet and to the southwest through Chincoteague and Assateague Channels (Fig. 1). Snow Hill Public Landing lies approximately at the point where the tides from the northeast and southwest meet. Test panels were submerged at this location from April 1952 through September 1953. Throughout this period no set of shipworms was encountered.

The station at Rattlesnake Landing was located approximately 4 nautical miles southwest of Snow Hill Public Landing. Test panels were submerged at this location from June 1950 through October 1952. Only a trace of *Teredo navalis* was encountered during 1950 (Table I); these shipworms appeared in August and September. In June 1951 a moderate set, 30 shipworms per panel, appeared. A set which occurred at Ocean City in July 1952 was not duplicated at Rattlesnake Landing, although a late strike of slight proportions (22 organisms in one of the panels) occurred in October.

The low incidence of *Teredo navalis* observed on test panels in Chincoteague Bay during 1951 and 1952 was substantiated in 1954 by an examination of waterfront structures. No living specimens were obtained except at two areas indicated by hatched circles in Figure 1. It must be concluded that no recent heavy set of *Teredo navalis* has occurred in Chincoteague Bay.

TABLE I. Number of *Teredo navalis* L. on panels at three stations in Maryland coastal waters, 1950-1953

Year	Ocean City	Rattlesnake	Snow Hill Landing
1950 (June 1-Nov. 8)........	136*‡	4*	—
1951 (Apr. 2-Nov. 30)........	373*	30*	—
1952 (Apr. 29-Oct. 30).......	30†	11†	0†
1953 (May 25-Sept. 27)......	—	—	0†

*These figures are the total number of shipworms encountered on a series of monthly panels throughout the period indicated. One panel was submerged each month at mid-depth.

†These figures are the average of a vertical series of panels submerged continuously for the entire period indicated. The data from Ocean City are based on nine panels. The number per panel ranged between 0 and 79 organisms (see Fig. 3). The data from Rattlesnake Landing are based on 5 panels with a range of 3-22 organisms per panel.

‡Ocean City station was started on July 2, 1950.

The comparatively low incidence of shipworms in Chincoteague Bay during the last few years is not readily explained. Salinities throughout the bay, during the course of the study, were consistently well above the lower lethal limits (9 0/00) for *Teredo navalis* as reported by Miller (1926). Because the maximum depth is only 8 feet, water temperatures in Chincoteague Bay fluctuate considerably and closely reflect changes of the air temperature. Fluctuation in water temperature may possibly be unfavorable to normal larval development. The predators of shipworm larvae are unknown, but Nelson (1925) has suggested that the ctenophore Mnemiopsis is an important predator of mollusc larvae. Little is known of the exchange of water between Chincoteague Bay estuary and the Atlantic, or its effect on the distribution of shipworm larvae. Weiss (1948) has shown that fouling organisms inhibit the strike of shipworms, and this may be a factor in the low incidence of set in Chincoteague Bay.

A summary of the magnitude of set for the three stations studied during the four-year period is given in Table I. The values given, based on a varying number of panels at each station, indicate the magnitude of strike during each summer season.

It is concluded from the data that the attacks of shipworms reached serious proportions in Ocean City harbor, but that the strike in Chincoteague Bay was not sufficient to cause substantial damage between 1950 and 1953. However, the fact that *Teredo navalis* has been found to occur in Chincoteague Bay suggests that adequate precautions should be taken in the construction of water-front structures.

The assistance of the following persons is gratefully acknowledged: G. Jensen, F. Longwell, H. Mister, F. W. Sieling, and A. D. Hains.

SUMMARY

1. The destructive family of marine molluscs, the Teredinidae, were observed in Maryland coastal waters during the years 1950 through 1953. *Teredo navalis* Linné is the species commonly found in the Chincoteague Bay estuary and at Ocean City, Maryland.

2. The set of *Teredo navalis* occurs during the months of July through October and occasionally as late as early November. The months of heaviest set vary. The heavi-

est sets at Ocean City occurred in August 1950, September 1951, and July 1952.

3. The magnitude of the set observed at Ocean City was greatest in 1951 and least in 1952. There was a substantial difference in the severity of the attack.

4. The set at Ocean City increased with increasing depth below mean low water.

5. The rate of boring at Ocean City was greatest the first few months after set, decreased during the subsequent winter, and appeared to increase the following spring.

6. A low incidence in the set of *Teredo navalis* was observed in the Chincoteague Bay estuary between 1950 and 1952. On the basis of our present knowledge, the reasons for this low incidence of *Teredo navalis* can be only a point of speculation. Adequate precautions in the construction of waterfront structures in Chincoteague Bay should be taken to prevent possible severe destruction in future years.

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A MODIFICATION OF THE PLASTER-CHARCOAL TECHNIQUE FOR THE REARING OF MITES AND OTHER SMALL ARTHROPODS

Various workers have been faced with the problem of developing suitable equipment for the observation and rearing of small arthropods. Essentially, the techniques are concerned with confinement of the animals in an enclosure into which is placed some moisture-holding material. Frequently the maintenance of the water supply requires constant handling of the containers by the investigator.

Recent interest in the life histories of mites has stimulated the development of special rearing methods. Michael (1883) used blotting paper in cells made from glass rings fastened to microscope slides into which he placed oribatid mites. He had considerable difficulty preserving moist conditions. Wharton (1946) using a plaster-charcoal substrate demonstrated its value in observations on a chigger mite. Jenkins (1947) describes the same general technique in the rearing of three chigger mites. Camin (1953) working on the life history of a snake mite used filter paper saturated with a KOH solution in plastic boxes to maintain humidity. During the rearing of oribatid mites, Sengbusch (1954) used small Stender jars with moistened filter paper keeping them in desiccator jars with a saturated $ZnSO_4$ solution. Moist paper in vials was used by Britt (1951) in the study of a collembolan. A modification of the chigger-rearing technique, using 2-dram vials filled to one-third capacity with plaster-charcoal mixture, was adopted by Rohde (1955) during observations on the life history of phthiracarid mites. It is a modification of this method which is described here.

The unique feature of this modification is the lucite cylinder of 1 cm inside diameter and 2 cm length which has four 0.5-cm ($\frac{3}{16}''$) holes at one end (Fig. 1). These cylinders are imbedded in a single mass of plaster in a container of suitable size for use under the stereomicroscope. This allows for ease in handling and makes possible close observation of one to several colonies of animals. The purpose of the holes in the cylinder is to facilitate entrance of the plaster mixture as well as to form a union of the mass, within each chamber thus formed, with the bulk of the plaster mass between the chambers.

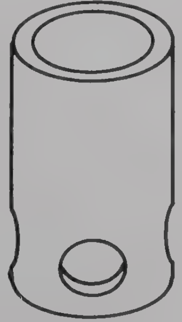

FIG. 1. Lucite cylinder.

In the making of a rearing box of this type, a plastic box with a snap cover is filled to a height sufficient to cover the cylinder holes with a dry weight mixture of 1 part activated charcoal to 9 parts plaster of Paris.

Water is stirred in to make a thick, soupy mass and then the cylinders are inserted with the aid of a template. A gentle tamping of the box completes entrance of the plaster mixture into each cylinder and aids the removal of air from the plaster mass. After the plaster sets, one

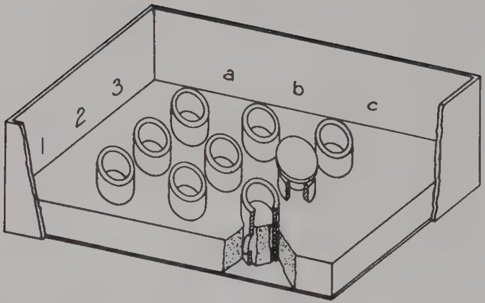

FIG. 2. Rearing box with cover removed. Section of chamber is indicated at 1c and at 2c a cork is in position.

has a series of life history chambers of uniform constuction and arrangement (Fig. 2).

Before the introduction of small arthropods into the chambers, the plaster-charcoal surface is scraped and tamped to eliminate minute holes and crevices which might serve to hide the animals and their developmental stages. When the surface in each chamber is completely smooth and free of openings and the cork in .position, a space of approximately 1 cc results. A No. 2 cork, so trimmed that very little of it enters the chamber, is used. The end of the cork must be smooth and free of openings.

The moisture-holding mass is thus continuous both within and between the rows of chambers. Water is added by merely dropping it on the plaster layer between the rows where it quickly enters each chamber. This eliminates the handling of many individual containers. To a large extent, condensation can be controlled by limiting the amount of water added. The hygroscopicity of the cork also helps to prevent droplets from collecting.

Addition of the cover thus gives a box which will hold moisture and can be handled and stored with little difficulty.

The size of cylinders and of the box can be varied according to the needs of the investigator. An ordinary plastic sandwich box, obtainable at a variety or hardware store, of 10 x 11 x 3-cm dimensions will accomodate as many as 25 separate chambers.

This technique has been successful in the rearing and handling of acarid, uropodine and phthiracarid mites and is equally useful in similar studies on collembolans.

The technique of rearing and subsequent studies on the life histories of soil fauna are of particular interest to this laboratory which is concerned with the effects of radionuclides and radioactivity on natural soil populations. Studies on the effects of radiation upon the developmental stages of these animals have made necessary the construction of special rearing chambers. Several types of rearing boxes have been built utilizing the above materials and principle of construction. Among these are models (1) which serve as both irradiation and rearing boxes obviating the need for transfer of animals; and, (2) which are used in such general observations as those on feeding, mating, oviposition, hatching, etc.

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A NOTE ON THE OCCURRENCE OF THE PINK SHRIMP *PENAEUS DUORARUM* IN LOUISIANA WATERS

Springer and Bullis (1952) first reported the pink shrimp *Penaeus duorarum* Burkenroad from Louisiana on the basis of its presence in two trawl collections made from the saline waters outside the Chandeleur Islands. During the course of the recent ecological survey of Lake Pontchartrain, a total of one hundred and four specimens of this species were taken in thirty trawl collections from Chandeleur Sound and from the brackish waters of Lakes Borgne and Pontchartrain. In addition, a single large (145 mm) female of this species, transmitted to the senior author by a commercial fisherman, Mr. Antoine Carrere, was taken from Bayou Grand Caillou of Terrebonne Parish on May 13, 1955, establishing the first positive record of the species from the Louisiana coast west of the mouth of the Mississippi River. All Louisiana specimens except those of Springer and Bullis have been examined and verified by the authors.

P. duorarum appeared in twenty-three collections made within Lake Pontchartrain (Fig. 1). Most of these collections contained less than three specimens although a single collection contained seven. All specimens from the lake were less than 120 mm in length and are considered juveniles and subadults. The pink shrimp first appeared in two collections from the lake in October and November, 1953, and although regular monthly sampling was conducted throughout the year, it did not reappear in collections from the lake until November, 1954. Thereafter the species continued to be taken in approximately one-fourth of the trawl collections through May, 1955, when sampling ceased. Physical data taken at the time of each collection reveal that the species was present in Lake Pontchartrain within a temperature range of 10.5-28.8°C and a salinity range of 3.9-10.3$^0/_{00}$.

The pink shrimp appeared in five collections from the

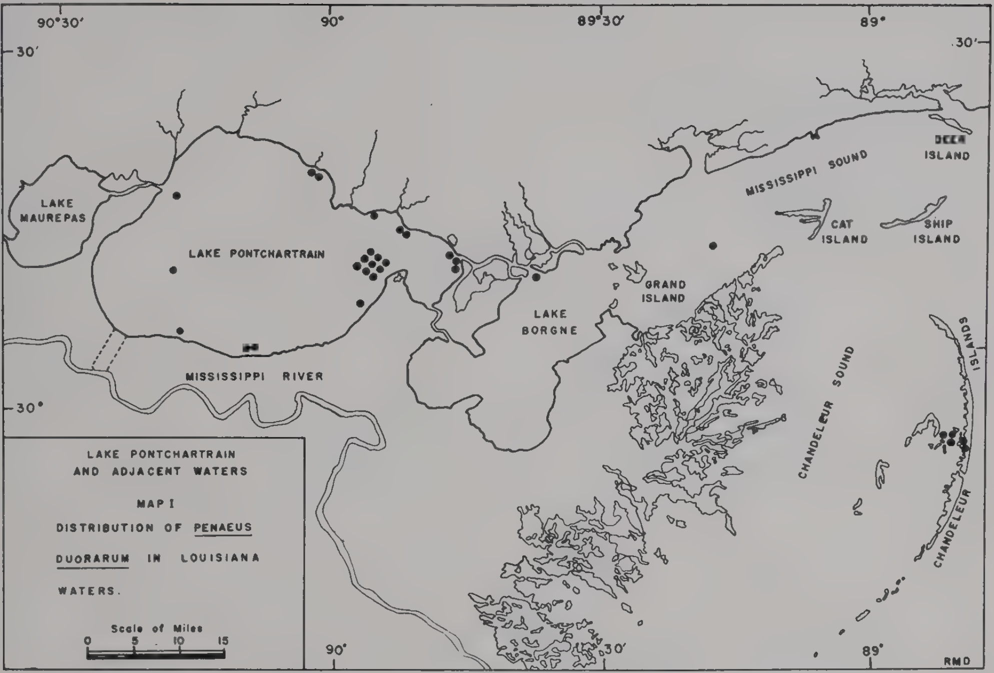

Fig. 1. Distribution of *Penaeus duorarum* in Loiusiana waters, 1953-1955.

Chandeleur Islands in March, 1954, and a single night collection from the lee channel contained thirty-nine specimens. All were subadults except one adult female (150 mm) whose ovaries appeared to be in the opaque "developing" stage (King 1948). The temperature range for these collections was 20.0-21.5°C, and the salinity range was 30.6-35.3$^0/_{00}$. Two collections from Lake Borgne in which the species appeared were made in March, 1953, and January, 1955, and physical conditions were intermediate between those observed in Lake Pontchartrain and Chandeleur Sound.

P. duorarum was found at all depths down to eleven fathoms which represented the deepest collections made in the area, and its greatest frequency appeared in two to three fathoms which is the depth range at which most of the collections were made. Bottoms within Lake Pontchartrain consist primarily of clay and silt with varying admixtures of sand, and an abundance of shells of the bivalve, *Rangia cuneata.* In the lee channel of the Chandeleur Islands the sand bottom is richly carpeted with calcareous algae and lime-coated aquatic vegetation. The single specimen of *P. duorarum* from west of the Mississippi River was apparently taken from a shell bottom inside the Derniere Islands.

Collections containing the pink shrimp frequently contained other congeneric species. Of the thirty collections from Lake Pontchartrain, Lake Borgne and Chandeleur Sound in which *P. duorarum* was present, nineteen contained the brown shrimp *P. aztecus* and thirteen contained the white shrimp *P. setiferus.* In nine collections all three species were present. The frequency of the pink shrimp (104) in the thirty collections was lower than the frequency of either of the other two congeners, brown shrimp (295), and white shrimp (225).

Until recent years the pink shrimp was unknown from Louisiana, and on the basis of presumed juvenile competition with its near relative the brown shrimp it was not expected to occur in the fresher coastal waters of the state, where the brown shrimp is abundant (Burkenroad 1939). Recent authors (Hildebrand 1954, 1955; Williams 1955) have emphasized the importance of differential habitat requirements rather than direct competition in limiting distribution and have cited instances of these two species as well as the white shrimp being found in the same area, either together or at different seasons of the year. Present evidence indicates that in the Gulf of Mexico the primary habitat of the pink shrimp is characterized by hard sand and calcareous bottoms rather than the less alkaline mud and silt bottoms upon which the brown shrimp is predominant (Springer and Bullis 1954; Hildebrand 1954, 1955).

Changes in the relative species composition of the commercial shrimp catch have been indicated for North Carolina waters by Broad (1950) and for Alabama and Mississippi coastal waters by Springer and Bullis (1952, 1954). In the latter case the pink shrimp appeared in abundance during the 1950 season but was virtually nonexistent in catches during the previous year and the following three years.

The presence of the pink shrimp in autumn 1953 collections from Lake Pontchartrain, and in spring 1954 collections from the Chandeleur Islands, indicates that the species was present in Louisiana waters at least a year before it began to appear frequently in the Pontchartrain collections. This fact, together with the widespread, diffuse nature of its occurrence during the winter of 1954-55, appears to indicate a temporary range extension into the lake during an exceptional year. Other species of invertebrates also differed in their patterns of occurrence within the lake during the two winters. Considerable hydrographic differences in the lake were recorded for the two successive years, and the data currently being processed may provide a more detailed explanation for observed changes in distributional patterns. Observed fluctuations in the physical environment appear to outweigh postulations of interspecific competition as the possible causative factors.

Sincere thanks is hereby expressed to R. D. Suttkus, chief investigator of the Pontchartrain project, to the Louisiana Wildlife and Fisheries Commission, and to the Marquette University Graduate Committee on Research for aid during the course of the work.

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COMPOSITION OF AN UPLAND CONIFER COMMUNITY IN ONTARIO[1]

The boreal forest types of Ontario are relatively unknown from a phytosociological viewpoint. In the summer of 1954, the writer was stationed in Algonquin Provincial Park and the opportunity of sampling a successional northern community was possible. Since no quantitative analyses of this community are to be found in the literature, it seems worthwhile to publish a few of the findings. The results of this study are to be incorporated into a broader study of the spruce-fir and spruce-fir-mixed hardwood communities around the Great Lakes, currently being undertaken by the author.

LOCATION AND DESCRIPTION OF STUDY AREA

The area concerned is centered around the point of intersection of the North Madawaska River and Highway 60, which is approximately 20 miles from the western boundary of the Park. (Lat. 45° 35′ N, Long. 78° 31′ W). The 5 stands sampled are situated within a 2 mile radius of this point (Maycock 1955).

White spruce (*Picea glauca*), white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), and black spruce (*Picea mariana*) are the dominant tree species of this type, which appears physiognomically uniform and is commonly found on sand plains in the area. These stands seem to have originated as the result of extensive fires and tree ring counts indicate ages of between 65 and 70 years. Tree cover is not uniformly distributed and many portions have a somewhat open-grown or woodland appearance. This distribution may be due to an irregular intensity of burning. Tree reproduction is largely confined to the areas where the tree canopy is less dense.

Weather records for Algonquin Park Station indicate a mean annual maximum temperature of 49.6°F, a mean annual minimum of 27.6° F, an average frost-free period of 111 days and a mean annual, evenly distributed, precipitation of 30.3 inches. The area receives an average annual snowfall of 91.3 inches.

These coniferous stands are invariably located on sandplains which are glaciofluvial and younger river deposits. Depth of bedrock of granitic intrusives is usually greater than 3 feet (Hills 1954). The soils, composed mainly of granitic sands with occasional gravel layers, show a characteristic podsol development with a 3 to 4 inch ashy grey A_2 layer. Profiles examined exhibited a 2 to 4 inch layer of raw humus, negligible development of the A_1 and usually sharply defined A_2 and B horizons.

METHODS

The criteria for the selection of stands were that they be on upland sites, at least 20 acres in size and free from recent fire, grazing, cutting or any other serious disturbances in the lifetime of the existing trees.

A preliminary cruise determined the extent, presence of disturbance and indicated the general condition of the stand. To judge homogeneity, a stem count of two major tree species was made along a 12 foot wide transect and the subtotals for segments of 100 paces in length were required to be equal within ± 20%. Any woody erect stem 3 inches d.b.h. (diameter breast height) or over was considered a tree, between 1 and 3 inches a sapling, and below this limit a seedling.

The quadrant method of survey as discussed by Cottam, Curtis, and Hale (1953) was used for sampling. Sampling points 30 yards apart along a compass direction were established and the nearest tree and nearest sapling to the point in each quadrant were recorded in the conventional way. Herbs and shrubs were recorded in meter square quadrats at every other point. Forty points per stand were taken, providing a sample of 160 trees, 160 saplings, and 20 quadrat records for herbs and shrubs. In the laboratory, relative frequency, relative density and relative per cent dominance were calculated for tree species. These 3 values were summed to give an importance value (Brown and Curtis 1952). Frequencies of herbs and shrubs were also calculated. Chi square tests (Snedecor 1946) applied to the frequency data for each stand indicated that none of the major tree species differed significantly from a homogeneous distribution. Nomenclature follows Fernald (1950).

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[1] The writer expresses sincere thanks to Dr. J. T. Curtis, University of Wisconsin, the Wisconsin Alumni Research Foundation, and the Department of Lands and Forests of Ontario.

RESULTS AND DISCUSSION

In the analysis, 18 species of trees were encountered. The 10 most important are listed in Table I and in addition to these, striped maple (*Acer pensylvanicum*), serviceberry (*Amelanchier* sp.), larch (*Larix laricina*), large-toothed aspen (*Populus grandidentata*), pin-cherry (*Prunus pensylvanica*), black cherry (*Prunus serotina*), mountain ash (*Pyrus americana*) and white cedar (*Thuja occidentalis*) comprise the total list. Of these, only serviceberry and pin-cherry were present in all 5 stands. The 10 species of Table I are most influential and confer the characteristic aspect to the tree stratum. The importance values form the main basis for a comparison of individual stands. Table II records the density and dominance per acre of all tree species per stand. White spruce and white pine have consistently high importance values in all 5 stands. This justifies the selection of these trees as the leading dominants of the community. The figures indicate a preponderance of white spruce but both species are outstanding constituents. These species may separately constitute over one-third of the ecological importance value per stand or two-thirds in combination. On this evidence, the community could be labelled a *Picea-Pinus* or *Pinus-Picea* type. Balsam fir is relatively important and possesses co-dominant status. This species is also very abundant in sapling and smaller tree size classes and its full importance is not therefore displayed. Black spruce appears also to be co-dominant. It is surprising that this species assumes the influence it has on upland sites but this is characteristic in this community in the region. Trembling aspen (*Populus tremuloides*) often occurs in small groves rather than entirely in a uniform mixture with the conifers, and white birch (*Betula papyrifera*) is often associated with it. Aspen is more abundant than birch but the larger basal areas of the latter are reflected in the similar importance values for these species. Red pine (*Pinus resinosa*) has consistently low values in all stands but specimens assume remarkably fine growth form and usually tower above their associates.

Due to the open nature of this vegetation, many of the conifers have retained the lower branches and appear open-grown. The data of Table II indicate that tree densities and dominance varied considerably from stand to stand, a condition due mainly to a varying density of tree cover throughout.

TABLE I. Summary of data for the 10 important tree species in the spruce-pine community, Algonquin Park, Ontario

Tree species	Stand number	Frequency % trees	Density % trees	Dominance % trees	Importance values	Frequency saplings
Abies balsamea	1	4.2	2.5	1.1	7.8	20.0
	2	27.4	28.8	9.6	65.7	60.6
	3	30.0	35.6	14.7	80.3	60.6
	4	11.8	10.0	4.3	26.1	60.6
	5	26.3	31.2	14.4	71.9	48.1
Acer rubrum	1	—	—	—	—	—
	2	—	—	—	—	—
	3	1.0	—	—	1.0	1.2
	4	2.8	1.9	0.4	5.1	3.1
	5	—	—	—	—	—
Acer saccharum	1	1.0	0.6	0.1	1.7	4.4
	2	—	—	—	—	—
	3	1.0	—	—	1.0	0.6
	4	1.0	—	—	1.0	0.6
	5	—	—	—	—	—
Betula lutea	1	1.0	—	—	1.0	—
	2	0.9	0.6	0.8	2.3	1.8
	3	—	—	—	—	—
	4	—	—	—	—	—
	5	—	—	—	—	—
Betula papyrifera	1	5.2	3.1	1.7	10.0	0.6
	2	15.0	11.9	11.4	38.3	1.9
	3	1.8	1.3	1.6	4.6	—
	4	2.8	1.9	1.4	6.1	0.6
	5	4.4	3.1	4.5	12.0	—
Picea glauca	1	29.2	33.1	35.5	97.9	36.9
	2	23.9	25.6	32.6	82.2	20.6
	3	28.2	28.8	38.9	95.8	11.9
	4	31.8	38.8	35.7	106.3	8.1
	5	27.2	28.1	39.0	94.3	15.0
Picea mariana	1	11.5	10.0	4.0	25.5	27.5
	2	3.5	3.1	1.6	8.2	9.4
	3	5.5	3.8	1.5	10.7	6.9
	4	21.8	18.8	13.6	54.2	19.4
	5	11.4	11.3	10.2	32.8	29.4
Pinus resinosa	1	5.2	3.8	6.1	15.0	1.2
	2	0.9	0.6	0.5	2.0	—
	3	2.8	1.9	5.3	10.0	3.7
	4	2.8	1.9	4.0	8.7	0.6
	5	1.8	1.3	4.4	7.4	—
Pinus strobus	1	37.5	42.5	47.7	127.7	5.0
	2	21.2	23.1	39.4	83.7	0.6
	3	20.9	17.5	33.4	71.8	3.7
	4	24.5	25.6	40.1	90.2	3.1
	5	18.4	16.3	22.9	57.9	—
Populus tremuloides	1	6.3	4.4	3.9	14.5	3.7
	2	6.2	5.6	3.9	15.7	3.1
	3	10.9	11.3	4.7	26.8	10.0
	4	1.8	1.3	0.5	3.5	0.6
	5	10.5	8.7	4.7	23.9	7.5

Frequency data for saplings is included in Table I. Balsam regeneration dominates the tree reproduction of almost all stands and is important even in those stands in which it is of lower importance in the tree layer. White and black spruce reproduction is next in importance. It is noteworthy that pine regeneration is considerably less abundant than pines in the tree classes, indicating decreasing proportionate influence in the next generation. General observations indicate that most of the conifers are reproducing favourably in the less dense portions of the stands. Aspen would seem to be less important in the future on the basis of sapling frequency. Reproduction of hardwoods was evident only in a few stations. Many maple cotyledons were encountered in quadrats but evidence of their successful establishment was not often observed. The invasion of maples would seem possible with any trend toward mesic conditions, especially with the readily available seed source which exists in the vicinity. The presence of hardwood stands with large specimens of white pine and white spruce scattered throughout, may be suggestive of the possible path of succession in this forest type in this area.

Presence and frequency data for shrub and herb species are listed in Table III. Although over 100 species

TABLE II. Density per acre and dominance per acre values for all tree species

Stand number	Density per acre	Dominance per acre (sq. in.)
1............	197	19,562
2............	277	20,312
3............	130	10,748
4............	195	14,935
5............	120	8,789

TABLE III. Presence and frequency data for the important shrub and herb species of the Algonquin spruce-pine community

Species	Stand 1	Stand 2	Stand 3	Stand 4	Stand 5
Apocynum androsaemifolium....	10	5	5	15	x
Aralia nudicaulis.............	25	60	15	35	15
Aster macrophyllus...........	55	35	5	x	5
Carex sp.....................	25	75	30	25	25
Clintonia borealis............	x	5	—	x	—
Coptis groenlandica...........	5	10	x	—	5
Cornus canadensis............	75	95	50	90	95
Corylus cornuta..............	15	20	35	20	30
Dalibarda repens.............	30	30	10	5	x
Diervilla lonicera............	10	10	20	20	10
Epilobium angustifolium.......	10	—	5	x	5
Galium triflorum.............	x	10	5	x	x
Gaultheria procumbens.........	15	x	5	45	10
Gramineae spp................	75	85	70	50	85
Hieracium aurantiacum.........	30	10	20	x	45
Linnaea borealis..............	—	2	—	5	5
Lycopodium annotinum.........	10	10	—	25	25
Lycopodium clavatum..........	20	35	50	35	25
Lycopodium obscurum..........	20	40	25	20	25
Maianthemum canadense.......	60	70	45	80	40
Melampyrum lineare...........	15	10	35	30	40
Polygala paucifolia...........	25	40	15	25	35
Pteridium aquilinum...........	10	15	5	x	x
Pyrola elliptica..............	10	5	10	x	x
Rubus idaeus.................	15	20	5	15	x
Rubus pubescens..............	10	15	5	x	x
Solidago canadensis...........	x	x	15	—	15
Streptopus roseus.............	5	5	—	—	—
Trientalis borealis............	65	70	30	45	45
Vaccinium angustifolium.......	50	40	85	65	65
Vaccinium myrtilloides.........	15	10	25	60	20
Viola papilionacea............	5	—	—	15	10

Other important shrubs—*Comptonia peregrina, Lonicera canadensis, Sambucu pubens, Spiraea latifolia,* and *Viburnum cassinoides.*

Other important herbs—*Anaphalis margaritacea, Aster umbellatus, Chimaphil umbellata, Dryopteris spinulosa, Epigaea repens, Gaultheria hispidula, Goodyer repens, Hieracium scabrum, Lycopodium complanatum, Lycopodium lucidulum, Oxalis montana, Spiranthes romanzoffiana, Cladonia rangiferina, Cladonia gracilis, Cladonia cristatella, Caliergon schreberi,* and *Polytrichum* spp.

of herbs and shrubs were recorded as present in the community, it is possible here to list only the more important members. Those listed certainly include the dominants of the lower synusiae. The herbaceous cover of the more dense areas differs somewhat from that of the more heavily wooded sections. The shrub layer forms a conspicuous element in this type but it is the low shrubs which are the main components. Lichens and mosses are characteristic, with the former occupying the open situations but the latter in more shaded locations. The epiphytic role of the mosses and lichens should also be mentioned.

As previously stated, samples of this coniferous type, from general appearances seemed quite uniform. The preponderance of the major dominants indicated a *Picea-Pinus* community of regional uniformity. The data which were collected objectively appeared to substantiate this opinion to some extent, but also indicated the variation which is inherent in different samples of the same vegetational type. Tree dominants arranged in order of decreasing importance yielded 3 arrangements when the first 2 species were considered, 4 arrangements for 3 species and 5 arrangements for 5 species. Similar variation was discovered in the understory. This internal variation suggests the inadvisability of labelling this community a specific type on the basis of leading dominants.

SUMMARY

A general review of geographical location, topography, climate, soils, geology, and past history of the Algonquin Region indicate the importance of these factors in the establishment of the coniferous community under consideration. Logging and burning, spruce budworm outbreaks, and invasion by a group of highly competitive herbaceous species are largely responsible for the appearance at present.

Various members of this forest type are very similar physiognomically and the data indicate that the same group of tree species; white spruce, white pine, and balsam fir, comprise the main dominants although not always in the same sequence of importance. The present regeneration indicates a continuation of this dominance.

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MODIFICATIONS IN DESIGN AND USE OF THE LIVINGSTONE PISTON SAMPLER[1]

Introduction

Obtaining vertically undisturbed samples of the uppermost loose flocculent sedimental layers of lakes involves several all-but-insurmountable problems. Recovery of the poorly consolidated sediments common to recent lake deposits received impetus, however, by way of the lightweight piston sampler for lakes recently described by Livingstone (1955).

The basic design of the Livingstone piston sampler will undoubtedly find application in a variety of collection operations. Vallentyne (1955) has suggested the use of a Davis peat borer-type lock to prevent the premature movement of the piston when the Livington device is used in compacted sediments. The modification suggested here, on the other hand, retains the original features of the Livingstone piston sampler and will, like the prototype, operate most effectively where the recent loosely consolidated sediments are desired.

Description of Sampler Modifications

Ordinary rubber stoppers have been substituted for the machined metal pistons with leather rings described by Livingstone. Through this substitution a saving in time and expense in construction of the sampler is realized. The rubber stoppers may be adjusted to fit the sampling tube with any desired tightness. This eliminates the need for the spring-pins used by Livingstone to hold the piston assembly at the lower end of the sample tube until the collection is to be made. The rubber pistons have the further advantage of being resistant to abrasion.

Two one-hole rubber stoppers are arranged in tandem, as are the metal-leather pistons of Livingstone, to achieve self-alignment and greater effectiveness. A ¼ inch (0.6 cm) fully threaded rod or bolt serves as an axis allowing for placement of the rubber stoppers between washers and nuts. The details are summarized in the accompanying figure. The nuts serve to compress and hold the rubber stoppers at any desired outside diameter (piston size). Stoppers should be selected which slip loosely into the sampler tube before they are compressed, *e.g.*, rubber stoppers 2.5 cm in depth and 3.7 cm by 3.0 cm in diameters (No. 7 size) can be adjusted to fit well in a sampling tube having a 1.5 inch (3.8 cm) inside diameter. On compression, rubber stoppers of this size relationship will assume an effective piston shape. The shape of the piston may also be altered through the size of the washers embracing the stoppers. The upper end of the bolt or threaded rod may be drilled and fitted with a ring for attachment to the cable which holds the piston assembly in a fixed position as the sample tube is pushed past the pistons into the sediment (Livingstone 1955).

Methods

The sampling tube adapter, which incorporates the notched extension rod connection described by Lichtwardt (1952), has been lengthened to allow the cable clamp and hook to come up slightly above the retaining pin of the sample tube. Completion of the sampling operation leaves the piston attachment ring at the level of the tube retaining pin. In this position, the piston attachment ring may be readily reached and the cable hook detached from the piston assembly without altering the pistons and sample. The pistons serve as stoppers for the upper end of the tube. The lower end may be satisfactorily closed off by a small plastic bag held in place by rubber bands.

In removing the sample core, two procedures have been employed. A rod, at least as long as the collection tube, with a rubber stopper piston at one end is used to push the core from the bottom of the tube while simultaneously pulling the pistons from the top. The sample is either poured into storage bottles or cut off at the desired intervals and placed in bottles, depending on the water content of the sediment. When the collection is handled in this manner a number of difficulties arise involving secondary compaction and vertical contamination of the sediment. "Secondary" is used here to indicate changes which are subsequent to the actual sampling operation.

The second method involves thoroughly freezing the tube with its enclosed sample core and circumvents most of the above problems. The frozen sample may be removed by running warm water over the tube until the core can be pushed out of the tube. This solidified core can then be cut into segments of the desired vertical separation with a saw, such as a hack saw or a carborundum saw, if the collection has a high sand content. Vertical contamination may be minimized, even in the case of liquid collections, by either washing away the outer part of the frozen core segments in running water or by cutting off the outside portions. An approach to a quantitative sample could be obtained, for example, by cutting the core into segments as thin as 1 or 2 mm followed by perpendicular cuts into wafers 1 cm square.

In climates where freezing conditions persist during winter months, a further refinement may be added to the freezing method of core removal and division. The core can be frozen at the site of operation before the sampler is moved from the vertical sampling position. The advantage offered by solidification at the sampling site is of especial significance with the Livingstone device, as the piston principle allows the sample to be started above the lake bottom, thus including a column of water. Freezing of such a sample before it is "tilted" or otherwise "disturbed" appears to provide a method of obtaining a reasonable approximation of an undisturbed sample of the most recently deposited loose flocculent sediment. In a sampling location where dry ice is available, immediate solidification could be accomplished in the field without climatic assistance.

Once frozen, the sampling tube with the core and rubber pistons left in place may be stored in a deep freezer until time is available for sectioning and examination or storage of quantitative segments in a suitable preservative.

When freezing is not feasible, the greatest source of secondary compaction and vertical contamination with the present device is in removal of the core. An expendable transparent plastic sample tube has been used to avoid this phase entirely. A clear plastic liner has been employed by Phleger (1951) in the free-fall coring tube sampler described by Hvorslev and Stetson (1946) for oceanographic bottom collections.

A clear plastic sample tube allows for visual analysis of the core. With visual reference to the location of the core in the tube or to layers of different texture and color, the plastic tube and its contained core may be cut systematically into sections as thin as 1 or 2 mm, or a desired section only may be removed.

If the clear plastic tube is not used in an expendable manner there are still several advantages over opaque

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[1] We are indebted to Dr. J. Iversen for his critical reading of the manuscript.

brass or aluminum tubes. The sample can be viewed directly through the plastic, leaving no doubt as to the success of the operation. This is of special importance if the sample tube is to be used as a transporting and temporary storage cartridge. The clear plastic sampling tube permits the observation and measurement of the extent and position of various bands differentiated by such characters as texture and color. Such measurements can be recorded rapidly on graph paper that has been placed under the plastic tube containing the collection (DeGeer 1942, 1950). These observations and measurements can be employed to obvious advantage in matching and comparing sedimentary levels. When the freezing method of core removal is not employed, these measurements may be used to estimate the extent of secondary compaction incurred during core removal.

We note with interest Brown's (1956) description of similar variations on the Livingstone sampler, which have just been published in this journal. Brown's pattern for a simple, non-machined head is ingenious and he quite rightly stresses the advantage of clear plastic tubing for visual inspection of intact cores. The importance of allowing the sample tube to fill with water before the sampling operation, not only to eliminate buoyancy but also to cushion the sampling movements is indicated by Brown.

SUMMARY

1. This communication describes the substitution of variably controlled rubber stoppers for the machined metal and leather pistons proposed in the original Livingstone sampler. The writers have found this to be a simplification in terms of use and construction.

2. An increase in the length of the metal sample tube adapter is proposed as a matter of convenience in detaching the tube and pistons at the end of the sampling operation without disturbing the collection.

3. The use of clear plastic sample tubes is suggested as a desirable modification having the following advantages:

a. Immediate check on the success of the sampling operation.

b. Visual accurate recording of the physical character of the sample is possible immediately after collection before the sediment is disturbed.

c. Following rapid freezing, the core may be divided into a closely graded series of samples by sectioning the plastic tube with its enclosed sample. This procedure minimizes the danger of contamination and compaction.

d. If the freezing procedure is not employed, the transparent tube permits measurement of compaction arising during core removal.

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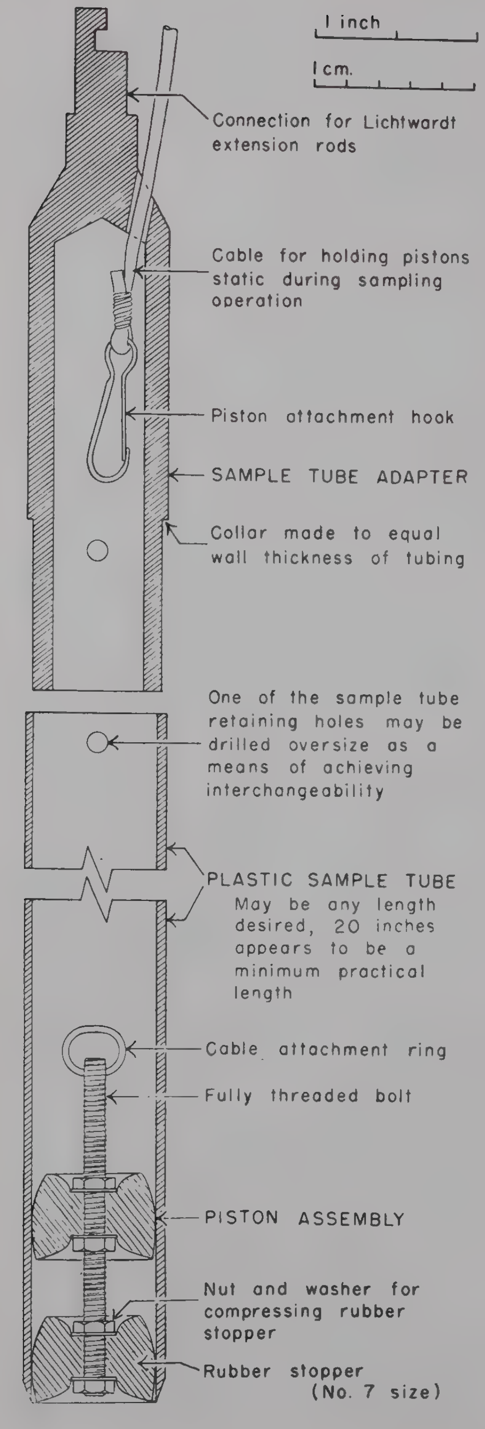
1 inch
1 cm.
Connection for Lichtwardt extension rods
Cable for holding pistons static during sampling operation
Piston attachment hook
SAMPLE TUBE ADAPTER
Collar made to equal wall thickness of tubing
One of the sample tube retaining holes may be drilled oversize as a means of achieving interchangeability
PLASTIC SAMPLE TUBE
May be any length desired, 20 inches appears to be a minimum practical length
Cable attachment ring
Fully threaded bolt
PISTON ASSEMBLY
Nut and washer for compressing rubber stopper
Rubber stopper (No. 7 size)

FIG. 1. Scale drawing showing the modified piston assembly and sample tube adapter for the Livingstone light-weight piston sampler for lakes.

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SUMMER FOG PRECIPITATION ON THE SAN FRANCISCO PENINSULA

The San Francisco Peninsula, like most of the central California coast, is dry in the summertime. Fields and hills turn yellow before May and even a trace of rainfall is rare in the summer months and often until November in the autumn. In spite of the dry summer aspect of the vegetation, fog almost daily shrouds the immediate coast line where the redwoods grow. However, only where trees are tall and exposed to blasting, fog-laden wind is there evidence of significant condensation.

The vegetation of the San Francisco watershed is relatively undisturbed and well represents this coastal fog belt. Here a trail or road may be dusty dry through grassland and chaparral then suddenly bog down in mud and pools of water beneath tall trees. On the crests of ridges where there is no high ground above for seepage, this summer fog precipitation is most striking. The wind blows fog against the branches of the tall trees of the ridge-top where it condenses and drops like rain on the ground below. The dripping is most evident under trees that are exposed and unprotected by any hills to interrupt the wind from the Pacific Ocean.

The first line trees to the seaward exposure receive the greatest amount of moisture and the trees to the east and down the slopes exhibit a gradual decline in this type of precipitation. An attempt was made to measure this source of water which appeared to contribute significantly to the ground water of this ridge.

Five totalizer gauges were made with a capacity of five gallons each and with straight sided funnels to collect the drippings. A one inch oil seal was placed in the cans to prevent evaporation. These gauges were placed under appropriate trees along a 3 mile stretch of Cahill Ridge. The gauges remained in place from July 20 until August 28, 1951. There was little chance of interference since the gauges were in a remote part of the enclosed watershed which is well guarded. Data concerning the relative positions of the gauges and the resulting precipitation are summarized below in Table I.

The gauges were placed at random beneath the trees, and there may have been some variation within the cover of any one tree. However, five gallon cans were used with at least 16 square inch exposure surface to minimize measuring errors. The 58.8 inch accumulation as found beneath the boughs of the tan oak represents a higher precipitation in little more than a month than found for the area in the entire rainy season. These trees must certainly play a prominent part in maintaining the ground water levels and the lower seepages noted on Cahill Ridge.

Table I. Precipitation under fog-exposed trees

Species of tree	Approximate height	Exposure position to fog	Inches of precipitation
Sequoia sempervirens	200 ft.	Forest, no front line exposure	1.8
Lithocarpus densiflorus	20 ft.	Direct exposure no interception of wind	58.8
Pseudotsuga taxifolia	125 ft.	Partly protected by Montara Mt. front line exposure	7.2
Pseudotsuga taxifolia	125 ft.	Little protected by Montara Mt. front line exposure	8.9
Pseudotsuga taxifolia	125 ft.	No protection by Montara Mt. front line exposure	17.1

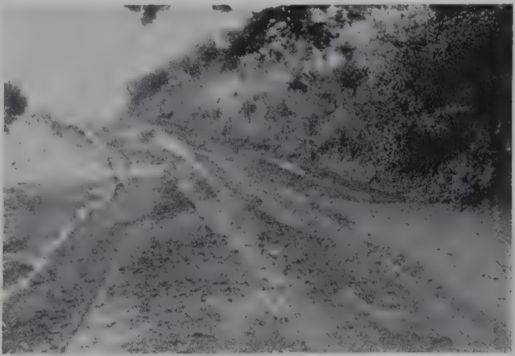

Fig. 1. Crest of Cahill Ridge in mid-July. Fog condensation from the Douglas fir in the background.

It is further evident that the position of a tree with respect to the interception of the fog-laden wind was perhaps more important, within limits, than the height of the trees in determining the amount of condensation. Adjacent grassland and chaparral had dry soil on the same days when this enormous precipitation was accumulating in the forests. Kittredge, (1947) in his summary of forest experiment station data, concludes that fog drip may increase the precipitation by 2 or 3 times that in the open. These data also show increased precipitation with the height and vertical expanse of the trees with maximum accumulation at the windward edge of the forest. Means (1927) sampled ground moisture under Monterey pine and eucalyptus and found an equivalent of 2 to more than 3 inches of precipitation from fog condensation under trees from 15 to 20 feet in height. He found that as the trees grow larger their collecting area shows a corresponding increase. Brush and grass, on the other hand, were found to collect relatively little.

Within these moist zones many early spring species continued bloming until late summer. The condensation appeared to provide the conditions for the orchids *Epipactis gigantea* and *Eburophyton austinae,* since these plants were found exclusively in these moist ridge tops. Although this fog drip is considered too spotty to be a limiting factor in coast redwood distribution (Byers 1953), it is evident that these hilltop pools add measurably to the floral variety. Seedlings of douglas fir, Monterey cypress, and eucalyptus appear to be encouraged beneath parent trees which collect moisture.

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COMPARATIVE YIELDS OF HERBAGE FROM OAK SCRUB AND INTERSPERSED GRASSLAND IN COLORADO

In much of southern Colorado and adjoining states, the lower foothills zone is covered with oak scrub and, since this is a cattle country often with short range, many have suggested that the oaks be cleared to increase the forage yields. Actually, relatively little clearing has been done, and there are few yield records where it has been done. It has also been pointed out that the forage under the oak scrub, which is largely blue grass, is very valuable forage late in the season and therefore it would be unnecessary to remove the oaks. The principal object of this study was to compare the yield of herbage from the oak clumps with the yield from grass parks outside the oaks. There was also opportunity to study the herbage yield from grazed land and from land ungrazed for the past 60 years. The ungrazed area enclosed a reservoir and a domestic water supply and stock had been fenced out.

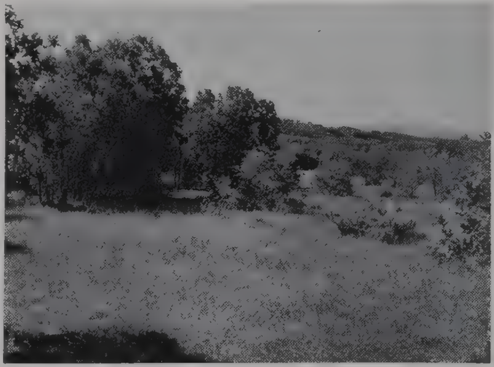

Fig. 1. Typical grazed oak scrub and grass-weed park range.

Site Factors

The study was made during the summers of 1944 and 1949 on Ft. Lewis range lands near Durango, Colorado, where the elevation is 7,700 feet. Figure 1 shows typical range land in the scrub oak community. The temperatures are mild and the precipitation averages 18.5 inches. The soils are light brown and classified as clay loam. Maximum noon light intensities from light meter readings in oak clumps varied from 40-200 foot candles while in the open they varied between 9,000 and 10,000 foot candles. The oak is Gambel's oak, *Quercus gambeli* and the dominant grass between the oaks over most of the area is western wheat grass, *Agropyron smithii.*

Soil samples for moisture were taken adjacent to typical herbage plots at one foot depths down to 6 feet and on the dates indicated in Figure 2. The parks tended to be lower in surface soil moisture early in June as compared with the oak clumps and about the same in moisture later in the summer. In contrast, the deeper horizons of the soil under the oaks lost more of their moisture during the summer than did the parks. The surface soil was near the wilting percentage of 6.8 per cent for both the oak and the park plots in September and early October. Soil sampling was not very satisfactory during the second season because of very dry conditions and difficulty in holding samples on the auger.

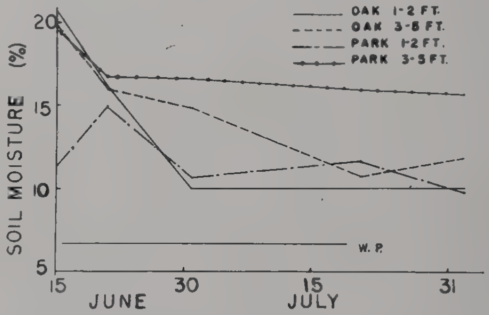

Fig. 2. Average soil moisture at the 1-2 foot and 3-5 foot levels for oak clump and the grass-weed park communities.

Methods

Samples of herbage were clipped from 25 square foot areas marked off in random fashion by throwing a wire ring into the area. Samples were from separate oak clumps and adjacent grass parks. The samples of herbage were placed in paper bags and taken immediately to the laboratory for dry weight determinations. Several representative open grasslands or parks and their adjacent oak clumps around a center within an area of 100 yards in diameter in the east half of the 10 square mile holdings were sampled the first season and a similar area one-fourth mile to the west was sampled the second season. Both of these pastures have been grazed for a number of years but there was no evidence of cropped herbage in any plot at the time of sampling and therefore no correction for use was made. The west pasture contained the enclosure for domestic water supply which has not been grazed for the past 60 years. The herbage clipped from each sample was classified and separated as (a) grass, (b) forbs, and (c) browse up to 4 feet from the ground for the oak clumps.

An attempt was made to determine the change in species as a result of grazing both by noting the species and their numbers in many of the circular plots. A 30 foot transect was also run in the ungrazed area and in the grazed area. The plants contacting the transect line were listed as to numbers of each species and their height after the method of Wilm *et al.* (1944).

RESULTS

As is indicated in Table I, the yield of herbage in the grazed pasture averaged almost twice as much for the 13 grass-weed park plots as for the yield of 11 adjacent oak clump plots. The yield for the oak areas includes browse up to 4 feet from the ground which makes up about half of the total oak herbage. However, oak leaves are usually spurned by most classes of livestock except goats. While the variation in yield of herbage from different plots was high, the difference between the yields of the open parks and the oak clumps was definitely significant. With a probability of 5%, the odds are 19 to 1 against this conclusion being a false one.

TABLE I. Average yields of air-dry herbage in pounds per acre

Class of vegetation	Grass parks Grazed range	Oak clumps Grazed range
Grasses	449.5†	179.0‡
Forbs	322.0**	27.8††
Browse	.....	198.3‡‡
Total yield	771.5*	405.1*
	Ungrazed range	Ungrazed range
Grasses	1133.7†	773.7‡
Forbs	237.8**	80.4††
Browse	.....	16.8‡‡
Total yield	1371.5	870.9

*$\frac{\text{Mean Deviation}}{\text{St. Error of Diff.}} = \frac{128}{59.6} = 2.14$

†Mixed intermediate and short grasses, including in largest numbers, *Agropyron smithii*, *Poa pratensis*, and more *Festuca* and *Muhlenbergia* where ungrazed.

‡*Poa pratensis* only.

**Mixed forbs, the most abundant being *Sphaeralcea dissecta*, *Achillea lanulosa*, *Eriogonum jamesii*, *Artemisia ludoviciana*, *Erigonum umbellatum*, *Erigeron flagellaris*, *Lupinus argenteus*.

††Forbs, usually limited to: *Taraxacum officinalis*, *Achillea lanulosa*, *Vicia americana*, *Lactuca* sp.

‡‡Oak leaves.

Also it must be noted that the forage in the grazed open parks tends to be somewhat on the less palatable side. Forbs formed over 40% of the dry weight of the herbage in the grazed parks, about 17% of the herbage in the ungrazed parks, while they formed only 6% of the dry weight of the herbage under the oaks or only 15% of the herbage if the browse were not considered. A few oak clumps yielded at a high rate where the scrub was so small as to make little shade but thick enough to decrease the feeding of cattle.

The 3 ungrazed grass parks yielded on an average only about 1.5 times as much as the adjacent ungrazed oak plot; and about 1.15 times as much as the grazed grass park plots nearby. Their herbage yield was about 1.77 times as much as the average of all grazed grass park plots. This shows only a trend in yields since there were not enough plots in the ungrazed area for satisfactory statistical treatment.

The 30 foot transect run on a typical ungrazed grass park yielded 58 plants with an average height of 7.1 inches including 37 *Poa pratensis*, 11 *Muhlenbergia montana*, 3 *Festuca arizonica* and 3 forb species—7 plants altogether. The transect through a representative area of grazed park yielded 92 plants with an average height of 3 inches. This included 56 *Poa pratensis*, 4 *Muhlenbergia montana*, 2 *Festuca arizonica*, and 18 forbs falling into 6 species. Apparently the *Muhlenbergia* and the *Festuca* were vigorous enough in the protected area to crowd out many of the forbs.

Grazing on the grass parks has had a tendency to decrease both the numbers and the kinds of plants and to increase the numbers of weedy plants most species of which would be rated according to Dayton *et al.* (1937) as poor to fair forage or even indicating overgrazing.

The intense light in the open areas with resulting high transpiration rates and loss of soil moisture at critical times as compared with the low light intensities under the oaks evidently account for the abundance of forbs in the open and the abundance of bluegrass under the oaks. The full explanation of the difference is not indicated but it is apparently not a case of general differences in soil moisture.

To solve the problem of forage production in the two types of communities, it will be necessary to take herbage yields on cleared oak land that has been reseeded to adapted species to compare with the yields of uncleared land. Koonce (1937) has made trials of cultivated grasses in this region. Hull and Johnson (1955), Reynolds and Springfield (1953), and Stewart *et al.* (1939) report similar tests in their recommendations for reseeding range lands.

ACKNOWLEDGMENTS

The writer wishes to thank E. H. Bader, Dean at the Ft. Lewis Branch of Colorado A. & M. College, Hesperus, for suggesting and promoting the study and G. E. Klipple of the U. S. Forest and Range Experiment Station, Ft. Collins, for suggestions regarding the manuscript.

SUMMARY

1. This study of a foothills scrub oak community shows that the yields of herbage average twice as great from the open grass-weed parks between the oak clumps as from the clumps themselves.

2. The forage under the oaks is of fairly high quality, being composed almost entirely of blue grass, while in the parks there are more forbs and drought and sun-tolerant grasses. With moderate to heavy grazing, there is a definite trend to the less palatable species while the Arizona fescue and mountain muhly decrease in number and vigor.

3. The results of this study suggest the desirability of further work with records of forage yields from land cleared of oak scrub and seeded to suitable range species.

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REVIEWS

FOREST HISTORY OF MIDDLE EUROPE[1]

Pollen analysis and its applications have attained a far greater degree of refinement in Europe than in the United States, as these two volumes demonstrate. By way of further evidence may be cited, in addition to numerous monographs and a vast number of journal articles the manual by Faegri and Iversen,[2] books by Erdtman,[3] and the serial bibliography[4] and new journal GRANA PALYNOLOGICA[5] issued by the latter.

The presence of some fifty workers at the Third National Pollen Conference held at Oberlin in May of 1956 is a measure of growing interest in the United States and an indication of our urgent need to come abreast of Europe. The recent visit of Professor Iversen to this country, the increasing number of American students who go to Europe for training, the existence of an International Committee, the development of several good laboratories for commercial research by oil companies, and of well-equipped centers at Harvard, Indiana, Michigan, Oberlin, Oregon, New York University, and Yale are all auspicious. But the facts remain that our country is vast, the subject did not begin to receive attention until some fifteen years later than in Europe, and mature American workers are subject to administrative and routine pressures greater than those of Europe.

An added factor not to be overlooked, is that pollen analysis is basically an ecological technique, and that ecology does not as yet receive the openhanded support in the United States that its potential importance deserves. We have no institutes comparable with those of Switzerland, Germany, and Scandinavia.

Thus circumstances combine to make the two volumes under review of especial interest to American workers, even though the area of consideration is Germany essentially, from northern Alps to the North Sea, and from the Juras and Vosges to Austria, Czechoslovakia and Poland. The combined bibliographies of the two volumes list well over 1500 papers, the work of several hundred authors. The references to these authors in the text give every evidence of care and intelligence in getting at essentials. The style is clear and direct, so that despite the imperfect command of German unfortunately too common among us, we may thank Professor Firbas for a means of saving us great labor.

Volume 1—General Forest History—begins with a few pages of excellent historical summary, followed by a section on methodology, with chief, but not exclusive emphasis on pollen analysis. The use of macro-fossils and cultural evidence is also discussed. Conventional generic and sediment symbols are shown. It has been standard European practice from the beginning to record sediments in pollen profiles.

Of especial value are the comments on the significance of non-tree pollen, of minor fluctuations and pollen concentration (frequency or density) and on sources of error due to distant-transport and redeposition. The importance and difficulty of critical pollen identification are duly noted. Happily there has been recent progress on this problem through the use of refined optical methods, but no one has yet come up with any royal substitute for long and tedious experience.

The general sequence of forest history (late and postglacial) occupies more than fifty pages of volume 1 and is of general value beyond the geographical area considered. Ten phases are recognized, marked by Roman numerals, and equated with European sequences elsewhere. The only references to American work are very general in character, no pollen profiles being considered although the sequence is substantially that of Europe. Correlative sources of data do not include Carbon-14, since the writing largely antedates its use.

Data on individual species, migration, and the changes associated with it occupy a major portion of Volume 1, while Volume 2 is devoted to detailed consideration of profiles from three main regions (1) the northern Alpine front, (2) the middle mountain region north of the Danube, and (3) the northern lowlands. The care and judgment shown here is a model of efficient abstracting and comparison.

Two important sections conclude the first volume, a review of the ten phases of late and postglacial climatic and forest history, and a consideration of prehistoric and early historical relations of man to forest history.

Northern American pollen analysis is now facing a change from its first exploratory phase to one of mature and critical detailed study. While it is essential that this work proceed independently and without preconceptions, it cannot afford to ignore the lessons so painfully learned by our colleagues in Europe. And since many signs now point to the possibility of important trans-Atlantic correlations, our laboratories will be well served by this impressive work of a modest, industrious, and effective European scholar.

For a detailed critical review based upon intimate knowledge of European conditions, the reader is referred to Iversen.[6]

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[6] Iversen, J. 1950. Late and post-glacial forest history in Central Europe. (A review) Oikos 2: 315-317.

An Introduction to Tropical Forests[1]

This little book is one of a popular science series edited by Professor Karl Frisch of Munich and is essentially a popular account of the vegetation of the humid tropics with special reference to the Malayan region with which the author is personally familiar. The book has no pretension to be a comprehensive scientific work and indeed in his epilogue the author refers those who would delve deeper to Richards' book—"wer tiefer eindringen möchte, sei verwiesen auf das Buch P. W. RICHARDS, 'The tropical rain forest,' Cambridge 1952."

On this level the book is good and readable and is effectively and clearly illustrated. The title is misleading in a sense, in that the whole range of vegetation of the humid tropics from mangrove and strand to high alpine is covered, and not only the rain forest in its strict definition. The author tends, too, to dwell upon the curious and extraordinary features of this vegetation rather than upon essentials, and expresses the awe and wonderment which it so often seems to excite in visitors from the temperate zone. This is perhaps to be expected in a popular work, particularly one emanating from Germany, since it is German writers who seem specially prone to the hypnosis of *tropischer Urwald*. To those who live and work for some years with the tropical rain forest, its special features fall into a different perspective. So also to those with experience of the extra-tropical vegetation of the southern hemisphere, where so many of the adaptations and characteristics that Professor Bünning describes are found well outside the tropical regions. The brief mention of the theory of continental drift (p. 88) shows that the author is not familiar with du Toit's reconstruction, from which it is possible to understand that the north temperate region was early separated from that of the tropics, while much of the south temperate has been in continuous contact with the latter, hence the greater similarity.

This book is on the whole a very satisfactory introductory account of a vegetation which has long been a source of wonderment to travellers from the northern hemisphere. The author is to be congratulated on the manner in which he has accomplished his purpose within a mere 116 pages and with a minimum use of technical terms and names.

J. S. Beard

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Pietermaritzburg, So. Africa

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[1] Bünning, E. 1956. Der tropische Regenwald. Berlin: Springer-Verlag. (Verständliche Wissenschaft 65) 116 pp., 116 Figs. DM 7.80, $1.85.

Water Balance of Savanna and Thorn Woodland[1]

This bulletin describes a comparative investigation of the water economy of two Brasilian vegetation types, based on transpiration studies. The two types compared were *campo cerrado* or savanna and *caatinga* or thorn woodland, the former at Emas in the State of São Paulo, latitude 22°S, altitude 575 meters, annual rainfall (1949-53) 1300 mm., 85% of which falls in summer (October to March); the latter at Paulo Afonso in the State of Bahia, latitude 9°S, altitude 250 m., rainfall 500-700 mm. with a highly erratic and uncertain distribution. This work is one of a number of papers on similar work, some by the same author, which reflect the influence of Professor Rawitscher in Brasilian ecology.

Transpiration rates and the rapidity of stomatic reactions were established by means of rapid weighings with a Jung torsion balance. Stomatal openings were analysed by Molisch's infiltration method with xylol or direct observation under a microscope. Cuticular transpiration and leaf saturation deficits were also estimated.

In the savanna leaves appeared to transpire freely more or less throughout the year, stomatal reactions were sluggish, cuticular transpiration rarely detected and saturation deficits low. In the thorn woodland, transpiration was found to be low even in the rainy season, and stomatal reactions rapid, the stomata remaining open for only a few hours in the morning. At other times a very low rate of cuticular transpiration took place. Saturation deficits were also low.

The vegetation of the thorn woodland is therefore clearly adapted to an arid environment while that of the savanna is not. On the other hand, says the author, the savanna vegetation is in general much more xeromorphic than the other, which is something of a paradox. He explains it in this way, that since transpiration in the thorn woodland is limited to short favourable periods it is important that photosynthesis should then be able to proceed freely. Access of light and CO_2 might be hindered by xeromorphic structures such as hairs and location of stomata in depressions which are found in savanna plants, whereas well exposed but very mobile stomata would take full advantage of favourable periods but close rapidly to avoid excessive transpiration during severe periods. This hypothesis does not, however, explain why xeromorphic structures should occur at all in the savanna plants, which tap abundant moisture reserves all the year round.

The intention of this study, so the author tells us, was to provide data for planned land use, especially afforestation. One wonders, however, whether it was really very informative. It is clear that the thorn woodland is making full use of very limited moisture resources and that the savanna is not fully using its more copious resources. This much is equally plain from the habitat factors described. The heat and drought of the thorn woodland, the lack of soil water reserves and the intermittent streams are surely sufficiently eloquent in themselves of the water economy of the vegetation. Similarly, a depauperate *cerrado* vegetation at the altitude and latitude cited and with an annual rainfall of 52 inches may be assumed not to be making full use of water resources, in support of which we are told that the soil beneath it is storing water equivalent to 3 years' precipitation.

The presence of savanna vegetation is therefore due to adverse soil conditions or fire (or both). In the locality of Emas it is stressed that there is nothing adverse about soil conditions, although the vegetation photographs reveal a very flat landscape which must always (under a high rainfall) be suspect for bad drainage. In such a case the savanna is most probably a fire climax, having succeeded forest destroyed by fire or alternatively having remained on the site, due to prevention by fire of succession after rejuvenation of the landscape by a new erosion cycle, from a previous period when a typical savanna soil was present. Other work on Brasilian savannas, e.g., Waibel in Geog. Review 38(4) 1948, shows that there are portions of the plateau where soils of impeded drainage underlain by concretionary ironstone do in fact occur and these may be taken to be the true home of the *cerrado* vegetation. Being fire resistant, the latter would tend to spread onto other soils where burning was a regular occurrence. The transpiration and so on of the savanna plants should properly be studied on a true savanna soil. One ventures to think that in such case the xeromorphic structures observed in savanna plants would be found to have some real adaptive value.

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[1] Ferri, Mario Guimaraes. 1955. Contribuição ao conhecimento da ecologia do cerrado e da caatinga. Estudo comparativo da economia d'água de sua vegetação. (English summary) Universidade de São Paulo, Faculdade de Filosofia, Ciências e Letras, Boletim No. 195 (Botânica 12), 170 pp., 100 figs.

J. S. Beard

Natal Tanning Extract Co.
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Soil Fungi in Relation to Root Disease[1]

"In any quest for the unknown, we unconsciously seek for, and expect to find, large differences and spectacular phenomena; disappointed of an imaginary mountain, it is possible to overlook reality within the compass of a molehill."

In this volume, the ecologist will find that many concepts developed in the fields of plant pathology and microbiology are applicable to the study of the ecology of natural vegetation and crop plants, and to applied ecology of many types.

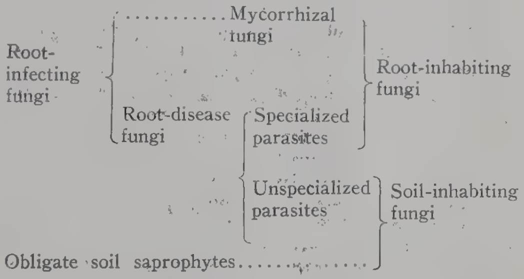
Garrett's earlier book, *Root Disease Fungi,* published by Chronica Botanica in 1944, was intended to be a comprehensive review of the literature on the subject. The present work is designed to present a summary of knowledge of those root disease fungi with which the author is most familiar. Emphasis is placed on results of studies with soil and root disease fungi which increase their importance not only in the field of crop ecology but also in the field of the ecology of microoganisms.

The *inoculum potential,* "the energy of growth of a fungus (or other microorganism) available for colonization of a substrate at the surface of the substrate to be colonized," required for infecting roots is greater than that for leaves where a single spore can initiate infection. Early attempts to produce root infection by use of pure cultures in infection experiments probably failed because insufficient artificial inoculum was used to produce an adequate inoculum potential.

The current "phase of microbial ecology" in the study of root diseases and the fungi which cause them, "began with the ultimate realization of the preponderant effect of other soil microorganisms in the environment of a root-infecting fungus." As a result of this type of study, soil sterilization and artificial inoculation of soils have become important methods in the attempt to deal with root disease fungi.

The biological control of root disease fungi in the soil is briefly reviewed. In this connection, the resistance of fungi like *Trichoderma viride,* a widely distributed soil saprophyte, to various soil disinfectants is described. In discussing the significance of antibiotic production by soil microorganisms, it is pointed out that proponents of the idea that antibiotics produced by soil organisms become diluted in the soil have not taken into consideration the fact that the antibiotic is required only in the immediate vicinity of the very fine threads of mycelium producing it.

Elaborating on concepts first developed by Waksman, and by Reinking and Manns, Garrett proposes two general types of fungi in the soil: "the *root-inhabiting fungi* are characterized by an expanding parasitic phase on the living host plant, and by a declining saprophytic phase after its death," and "the *soil-inhabiting fungi* are characterized by ability to survive indefinitely as soil saprophytes." It is pointed out that in order to be classified as a soil-inhabiting saprophyte, a parasite must be shown capable of colonizing dead organic matter buried in unsterilized soil. The following scheme relates root-infecting fungi to other soil fungi:



In studying the synecology of soil fungi, the state of occurrence of fungi as spores, resting cells, or active mycelium, and enumeration of these fungi have been considered of great importance. These problems are becoming more and more unreal as questions remain unanswered. Techniques are being developed to discover more realistic alternatives in the study of soil fungi. Direct observation of soil fungi amounts to observation of actively growing mycelium rather than actively sporulating structures. "With the plate count method one identifies what one cannot see (i.e., *in situ*), whereas with the direct method one sees what one cannot identify."

Not only microfungi but macrofungi have been studied from the point of view of synecology, but while the latter are usually sampled as if they were higher plants, the former are sampled in so crude a fashion as to obscure all variations of the fungus flora. Garrett says, in connection with present techniques of sampling the soil fungi: "The limitations of such a technique for study of the soil fungus flora can only be appreciated by imagining the vegetation above ground of a meadow to be investigated solely by means of samples taken from a haystack."

A more rational approach to the ecology of soil fungi is suggested in the form of a study of substrate relationships using "substrate" both in the sense of plant and animal bodies or tissues supporting growth and of the nutrients required for such growth. Substrates for such fungi are discontinuous in time and space. The rhizosphere of living roots is an example of a substrate discontinuous in space. The root of a host plant is an example of a habitat discontinuous in time: the living root supports a root surface and rhizosphere population; the root may become invaded by parasitic fungi which pave the way for saprophytic sugar fungi, cellulose-decomposing fungi, and finally lignin-decomposing fungi. The orderly development of such a succession will become better understood as techniques for fungal detection improve. The demonstration of this succession by gross agar plate technique will lead to confusion. The study of a sere leading to a climax of higher plants begins with a bare area in which conditions build up to a state at which a climax can be supported. With the growth of microorganisms the substrate is gradually depleted so that the succession eventually results in zero.

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[1] Garrett, S. D. 1956. Biology of Root-Infecting Fungi. New York: Cambridge University Press. xi + 288 pp. 1 fig., 9 tables. $5.50.

Pathogenic soil-inhabiting fungi have been defined as primitive parasites which can survive indefinitely as soil saprophytes. Primitive parasites include those fungi capable of infecting immature or aging roots of seedlings or plants. Since successful parasitism involves a minimum disturbance to host tissues, the efficiency of a parasite can be correlated with the degree of symbiosis the parasite achieves with its host. Thus the most successful parasites are the ectotrophic mycorrhizal fungi. The minimum destruction of host tissues occurs with parasites which have evolved far enough to overcome even the resistance of mature host plants in full vigor. The following possible evolutionary sequence of development of pathogenicity in fungi is suggested:

Primitive parasites	Restricted by mature host tissue resistance	Destruction of seedlings and juvenile tissues.
Less primitive parasites	Less restricted by effective host resistance	Rapid and less limited destruction of host tissues.
Specialized parasites	Some degree of temporary symbiosis with host	Reduced or delayed disorganization of host tissues.
Mycorrhizal fungi	Complete symbiosis	No destruction of host tissues, though hypertrophy may be induced.

Evidence to date indicates that the known pathogenic soil-inhabiting saprophytes are parasites of a relatively primitive type. Few can initiate destructive diseases in mature healthy plants growing under good conditions.

Garrett is of the opinion that "the very term 'obligate parasite' is not so much an objective biological definition, but a subjective admission of human failure to culture such organisms *in vitro*." He suggests that the root-inhabiting fungi demonstrate an intermediate type of behavior, and suggests the term *ecologically obligate parasites* for them. Biologically the mycorrhizal fungi can be arranged in an ascending order of parasitism, suggesting to some workers an evolutionary sequence. This might be the case if a morphologically distinct group of fungi were involved, but the mycorrhizal fungi are very diverse morphologically. Ectotrophic and endotrophic mycorrhizal fungi are discussed at length, and it is indicated that there is increasing evidence that the former are ecologically obligate parasites and that the latter include species with the ability to be saprophytic.

Root-infecting fungi exhibit several types of dormancy. "Physiological heterogeneity amongst a society of resting spores is a population characteristic having biological survival value." Under such circumstances, *decoy plants*, in the presence of whose roots the resting cells of root-infecting fungi can germinate but cause no infection, have been used to remove many of the resting cells present in an infested field. Several types of sclerotia are discussed, and the sclerotium of *Phymatotrichum omnivorum*, the cause of cotton root rot, is described in detail.

Mycelial momentum may be defined as "the product of effective mass of fungal inoculum and the velocity of fungal growth outward from that inoculum." *Host resistance* is a genetic property which may be demonstrated by the ability of a host to develop a defense mechanism. On the other hand, *disease escape* may occur on soils unfavorable to the mycelial activity of the infecting fungus, in soils in which an infecting fungus is absent, or in soils so treated that the type of growth of the host roots precludes infection by fungi that may be present.

"The degree of unrealized root damage is only appreciated after the spectacular results often obtained when crops are grown with really healthy root systems, following efficient soil disinfection."

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MARINE AND FRESH WATER PLANKTON[1]

There has been during the last decade or more an upward surge of interest in the sea. Several recent texts have appeared that include chapters or discussions pertaining to the plankton and its significance in the biology of the aquatic environments, but none professing to deal exclusively with the plankton has appeared for many years, despite an obvious need to develop the study.

There are nine chapters: 1, Introductory; 2, Special adaptions to planktonic existence; 3, General cycle of production in aquatic environments; 4, The phytoplankton (There is no special chapter on zooplankton); 5, Phytoplankton-zooplankton interrelationship; 6, Distribution problems; 7, Geographical and seasonal variations of structure; 8, Food of plankters; plankters as food; and 9, The kinds of plankton organisms. The book is based upon a summer's session of lectures and laboratory work and is evidently intended mainly for advanced college students.

As the title indicates, an attempt is made to deal simultaneously with two strikingly different and complex environments and their planktonic communities. The inclusion of both the marine and fresh-water fields within the confines of a single book of this size (342 pages of text including glossary, bibliography and index) seems unfortunate for it has led to restrictions in subject matter without much compensating effort at integration of the two fields.

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[1] Davis, Charles C. 1956. The marine and fresh-water plankton. East Lansing: Michigan State University Press. xi + 562 pp., 539 figs. $10.00.

The first 25 pages deal with some of the usual physical-chemical factors of the environments and with the evolution of lakes. About two-thirds of these pages are devoted to the fresh water environments; however, in most other sections of the book the emphasis is on the marine population. Included is an especially good discussion of the floating adaptations, such as small size, spination, air bladders, etc., as they apply to both fresh-water and marine plankton in general. Adaptive life histories are also touched upon. The controversial subject of relative production in offshore versus inshore and arctic versus tropical waters is dealt with, stressing the need for continuous observation to eliminate the discrepancies due to seasonal aspects. The phenomenon of diurnal migrations is well covered in Chapter VI, but for most advanced students in marine biology it will seem strange that in this connection no mention whatever is made of the association of plankton to the deep sound-scattering layer.

Included (in Chapter VIII) is a brief discussion of the nutritive value of plankton and of the methods of feeding by some characteristic planktonic animals and how they, in turn, are fed upon by filter-feeding forms such as the sardines, baleen whales and clams. Chapter IX comprises nearly one-half of the total text. It reviews the characteristics of the phyla, giving brief summaries on general morphology, affinities, and life histories. A number of artificial keys are given for planktonic genera of different groups. These should prove useful for preliminary analysis. The 618 figures, a little less than ¼ of which are original, make up a conspicuous part of the book. The radiolaria and coelenterates are given a disproportionately large consideration, having 80 and 92 figures respectively as contrasted to 32 for diatoms and 63 for copepods, the most abundant and ecologically important groups of the general community. The reader cannot fail, however, to be impressed by the beauty and intricacy of design in the radiolaria shown. The purpose of the figures in general would have been better served had the captions (31 pages) not been listed separately.

A number of ambiguities and errors have crept in; for example, p. 23 "for all practical purposes light can be said to be absent below 200 meters." This is hardly in keeping with known marine phenomena such as vertical movements of deep plankton in response to light. Fig. 16 shows the main current of the Bering Strait and eastern Bering Sea as a southward flow, an error which need not be perpetuated in light of surveys of the last two decades. On pp. 57 and 63, "littoral pelagic" is a confusion of terms. On p. 65, the phenomenon of "upwelling" appears not to be distinguished from local "turbulence" in East Sound. The use of "depth" for an oceanic "deep" is another deviation from oceanographic usage of terms.

There is a bibliography of 307 entries, 12 of which are later than 1950. A good index is provided.

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BLACK FLIES (SIMULIIDAE) OF GUATEMALA[1]

Black flies are pestiferous to man and animals due to their bites and as vectors of the filarial parasites which produce onchocerciasis. Human onchocerciasis is endemic in Central Africa, Guatemala, Mexico, and Venezuela. It is estimated that 25,000 Guatemalans are infected and that 35 per cent of the population is infected in disease zones.

Dr. Dalmat has defined the onchocerciasis zones in Guatemala and has attempted to associate them with various ecological factors including topography, climate, customs of the inhabitants, and biology of the simuliids. Onchocerciasis is most prevalent among workers on the coffee plantations. The coffee harvest period, when many men, women, and children are in the fields, coincides with the season of greatest black fly population. It is common to see men working on drying patios with thousands of flies feeding on their bare backs. Host preferences of the various species of black flies were determined by collecting biting flies from the exposed bodies of humans and various kinds of animals. Of the 41 species of Simuliidae known to occur in Guatemala, eight were commonly found to bite man, and three of these, *Simulium ochraceum, S. metallicum,* and *S. callidum,* are considered to be the principal intermediate hosts of the human parasite, *Onchocerca volvulus.* Detailed life histories are given for these three species.

Taxonomic keys, detailed descriptions, and good illustrations are given for the immature and mature stages of all species of Simuliidae that occur in Guatemala. Although no new species are described, many of the life stages had been previously undescribed or incompletely described.

Ecological data presented for the immature forms include ranges of altitude, water temperature, pH, width and depth of the stream, velocity, dissolved oxygen, substratum, and plant and animal associations. The larvae and pupae of different species are adaptable to widely different stream conditions. The habitat preferences of the various species were determined by analysis of approximately 4,000 collections from 510 streams throughout the country. The principal anthropophilic species prefer streams which are narrow, have a low flow, a stream bed that is earthen to arenaceous, and with abundant vegetation coverage and emergent vegetation to serve as anchorage. The zoophilic species prefer "older" streams with a larger flow, a stream bed of gravel and rocks, and a paucity of emergent or cover vegetation. Some forms inhabit pools of almost stagnant water and remain unattached on muddy bottoms. Various species of insects, fish, and birds prey upon the simuliids, and cases of parasitism by nematode larvae and Protozoa are described. The fish *Profundulus punctatus* was the most important predator, but due to the enormous breeding potential of the flies and the constant reduction of the fish by the Indians, who use them for food, their effect on the over-all fly population is considered small.

Flight range and longevity of the adult flies under natural conditions were studied by the release and re-

[1] Dalmat, Herbert T. 1955. Black Flies (Simuliidae) of Guatemala. 425 pp., 1 map, 44 plates, 21 figures, 36 tables. Washington, D. C.: Smithsonian Miscellaneous Collections, Vol. 125, No. 1.

capture of stained females on 75 different days. The life span of uninfected adults was concluded to be 3 to 85 days. Infection with *Onchocerca volvulus* reduced both longevity and flight capacity. Relative humidity was considered the environmental factor which most affected life span of the adults. The flies travel considerable distances and at rapid rates. Some specimens were captured nearly 10 miles from their place of release. One specimen of *S. metallicum* was recovered 3.8 miles from the release site during the day following its liberation.

The various species showed differences in preference of feeding times and in the relationships of air temperature and relative humidity to feeding habits. Contrary to the popular belief that the flies will not bite indoors owing to inadequate light, *Simulium ochraceum* frequently and *S. metallicum* occasionally bit humans inside of the laboratory at night when the reflected light from an electrical source was not more than two foot-candles. The optimum intensity of reflected light during which the anthropophilic species fed was between four and ten foot-candles.

Dr. Dalmat's excellent monograph on the Simuliidae of Guatemala is based upon his nearly six years (1947-1953) of field and laboratory studies on the flies and their role in the transmission of *Onchocerca*. The report may be criticized for being repetitious, but repetition is difficult to avoid when combining so many facets of a study of this magnitude.

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Mosquito and Dragonfly Manuals[1, 2]

Notice of the publication of the comprehensive systematic treatment of any group of organisms always comes as welcome news to the ecologist, particularly if that work is amply keyed, profusely illustrated, and includes information on all life-stages. Two recent books on important groups of insects, the mosquitoes and the dragonflies, are particularly praiseworthy in all these respects.

The mosquito volume[1] is essentially an up-dating and geographical expansion of earlier systematic works on the subfamily Culicinae. It develops the culicidologists' tradition of thoroughness and precision in both keys and illustrations to a degree that has probably rarely been equalled in this country for any animal group and at the same time shows sensibly little deference to the excesses of infracategorization that have occasionally been applied. The majority of space in the book is, of course, devoted to the standard taxonomic material, namely synonymy and careful but concise descriptions of the adult male and female of each species. In addition, an equally detailed description of the larva is included, followed by a brief summary of distributional records (listed by state only), and, where available and appropriate, a few comments on medical importance and "bionomics." The last category includes all details on the occurrence and activities that would, at one time, have been called natural history. While introductory explanations are quite brief and ecological information scant at best, the book unquestionably represents a milestone for the systematist and ecologist alike; for it is probably the first time that a single insect group has been so completely and presentably wrapped up in a single volume.

The Needham and Westfall work[2] brings the earlier handbook of Needham and Heywood[3] up to date (although this is in no sense a new edition of that one) and adds a very commendable series of photographs showing terminalia of all species and a general view of a nymph of each genus. Line drawings of the wings of all genera are also included. The book lacks much of the ecological material that greatly enhanced the introduction of the older work and omits the damselflies, which are reportedly to be the subject of another volume. While adequate (though somewhat abbreviated) in taxonomic detail, the book is aimed primarily at the collector and makes its major contribution in the many new illustrations and in the inclusion of keys (to species in nearly all cases) and descriptive data (at the generic level) on the nymphs. The great quantity of new material on the immature stages makes this book an extremely valuable addition to the literature of aquatic biology.

If either of these volumes has a fault, it is that the very admirable illustrations have been carried to excess—not to the disadvantage of the books themselves, but to the point that their prices place them out of reach for the usually impecunious devotees of these insect groups. It is quite possible that the full-page plates of the female of each species of mosquito could have been very effectively replaced by a smaller number of text figures of diagnostic details, and that the general photographic views on many of the odonate nymphs could have been shown more definitively by smaller outline drawings. The ecologist who is belabored by incomprehensible keys can well be thankful for the standards that these volumes have set, but he must continue to urge that a sensible balance between price and visual aids be sought.

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[1] Carpenter, Stanley J. & Walter J. LaCasse. 1955. Mosquitoes of North America (North of Mexico). Berkeley and Los Angeles: University of California Press. 360 pp. + 127 pl. $10.00.

[2] Needham, James G. & Minter J. Westfall, Jr. 1955. A manual of the dragonflies of North America (Anisoptera), including the Greater Antilles and the provinces of the Mexican border. Berkeley and Los Angeles: University of California Press. 615 pp. $12.50.

[3] Needham, James G. & Hortense B. Heywood. 1929. A handbook of the dragonflies of North America. Springfield, Ill., and Baltimore, Md.: Chas. C. Thomas. 378 pp.

THE MIND OF THE SPIRIT: E. A. BIRGE[1]

Academic lives are uneventful, and the world's indelible footprints are seldom made by professors. Probably the first American limnologist since Thoreau to merit a full-length biography, Edward Asahel Birge (1851-1950) proves an interesting but not altogether satisfactory subject. That the distinguished man of science was eminently worth memorializing is shown by the result: we have before us the very likeness of Emerson's American scholar, the fully educated man of action. Student of Agassiz, limnologist, professor, dean, university president, and grand old man—the public career is documented here. But what sort of man stood behind the craggy façade of the scholar-administrator? On matters that might illuminate the personality the author preserves a reticence that is no less disappointing for its conformity with Birge's own behavior.

No doubt it is too much to expect that a professional historian, dean, and academic colleague should master overnight the synthesis of psychology and art that successful biography requires. The book is correctly described as a memoir, and is not to be taken as biography in the modern sense. Within its limitations it is a useful and informative work. A generation of ecologists to whom Birge is but a name, a sort of separable prefix in the combination Birge-n-Juday, may find here both instruction and inspiration. An older generation, which has grown up in full awareness of the scope and vigor of Wisconsin limnology, may learn with genuine astonishment the prodigies of Birge's career.

Limnology was almost an avocation, fundamental as Birge's contribution was; it began after the age of forty, was pursued in intervals during a long career as academic statesman, and received his full attention only after his retirement from the presidency at the age of seventy-four. To judge from the evidence presented here, his numerous addresses on literary and educational subjects, like his memorials to eminent citizens and friends, display the vigorous and imaginative style that makes his scientific papers a pleasure to the eye and ear as well as to the mind. Schooled in the classics, a wide and discriminating reader throughout his life, his essays combine in a unique way a dazzling aptness of quotation, a homely simplicity, and a deep respect for the truth.

Birge's religious side will come as a surprise to some, and his interest in St. Paul (on whom he preached an annual lay sermon for thirteen consecutive years) seems throughly to have baffled his colleagues, including Dean Sellery. In the light of the remarkable letter to Mrs. Peckham (unfortunately the only private paper to receive extended quotation) the fascination of St. Paul may indeed seem puzzling; the letter reveals a complete latter-day Calvinist, the epitome of in-the-world asceticism, as unlike St. Paul philosophically as he may have been like him personally. If a theologically naïve reader may venture a guess about this paradox, it is that Birge respected St. Paul as the ranking stylist of all time, and rationalized the philosophy as greater theologians have done.

By a stroke of publishing genius as happy as it now seems inevitable, the chapter on Birge's accomplishments in limnology was written by Clifford Mortimer. It is a faultless piece of exposition, a work of art as well as of science, and thus a consummate tribute to the master naturalist. In outward form an essay on limnology for the general reader, and so successful that it can be used as a college text, it is far more than that. Birge's contributions are interwoven so skilfully that one realizes with a start that Birge's work and modern limnology are one and the same—there is no corner of the science that Birge did not illumine, and the whole subject bears the stamp of his personality as clearly as its parts show the force of his intellect. The fact that he was anticipated in some important respects and mistaken in others is as irrelevant for Birge and limnology as the same fact is for Darwin and evolution; to a degree that may never again be true of a single man, Birge was a man who founded a science.

To have made this achievement clear, without hyperbole and with exact justice to Forel, Wesenberg-Lund and Thienemann, is a rare tribute and an extraordinary accomplishment. Perhaps it could only have been done by a limnologist whose career, like Birge's, has moved from Cladocera to hydrodynamics to academic administration. No doubt, too, Mortimer's transatlantic detachment has been profoundly helpful, as has his spiritual kinship with Birge's nonconformist ancestors. At any rate, if the reader of Dean Sellery's chapters wants to know what happens to Birge's personality and character, which seem somehow to have got lost among the funeral orations, Mortimer's chapter gives at least a partial answer: they are not to be sought in administrative memoranda, or even in his sermons on St. Paul. The key is provided by Birge's quotation, "Infinite riches in a little room," and his character is best understood by those who really love and understand Lake Mendota.

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[1] Sellery, G. C. 1956. E. A. Birge. A memoir; with an appraisal of Birge the limnologist, *An explorer of lakes,* by C. H. Mortimer. Madison: Univ. Wisconsin Press, vii + 221 pp., 7 pls. $3.50.

A BRITISH ECOLOGIST'S LOOK AT AMERICA[1]

To the reader familiar with the characters and scenes Darling's odyssey will provide delightful light reading, but even to one who finds them more or less new the gems of thought will not be less rewarding. Darling is among those rare individuals who approaches Aldo Leopold's literary genius in forceful expression of deep, thought-provoking ecologic analyses and concepts. The contributions to philosophical ideas regarding interpretation of ecologic situations and conservation of land and its resources in America will be the lasting features of this book.

The flavor of the book can be illustrated by some of the following quotes: page 161—"The White River Apaches are not yet using their range entirely for their own stock, but are leasing it to white pastoralists who are not giving it proper care. What, finally, is to happen? Personally, I feel as pessimistic here as at home in the Highlands; you can only wait till all possible profit from exploitation has been squeezed out, and that such country should then be left alone. . . . page 166—prices for cattle are exceedingly high, so the game of shunting the cattle about is profitable, however suicidal a policy it is biologically. One thing much more obvious here than at home is that agricultural or pastoral prosperity means accelerated ill treatment of the land. . . . page 196—We came to slopes clear of snow on the north side of the Yellowstone Park and the degree of overgrazing and overbrowsing is rather frightening for the future. . . . The Roosevelt ethic of never shooting a doe is hard to modify. . . . We have got people educated to care for animals, now we have to teach them how to look at country and to shout when they see it being ill-treated. . . . page 204—It is the old story: once you cut into your humus layer on limestone, it disappears like snow upon the desert's face and the active limestone does not allow a new layer to build up. You are left with semi-desert. . . . page 281—Wild sheep, like any others, do better when they are not stocking their range to capacity. It is almost certain that the high numbers of the 1920s took their natural consequence in the crash of the early 1930s. . . . page 323—The skuas come in and gorge on the harvest of lemmings laid bare by the melting snow. The snowy owl does the same. . . . page 368—and the wild Alaska beyond is also just what suits me—indeed, it feeds me."

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[1] Darling, F. Fraser. 1956. Pelican in the wilderness. 380 pp., 15 plates. New York: Random House Inc. $5.00.

The principles expressed apply elsewhere than in America, and the book is enriched by generous comparisons with the Highlands of Scotland and other parts of the British Isles. Readers on both sides of the Atlantic will find much interest and understanding through this comparative approach. Human behavior and relations to natural communities have not been neglected in this respect. Indeed, one is deeply impressed with Darling's sincere interest in the human animal as well as wildlife and his vivid interpretations of real human ecology.

Little is spared by way of description and criticism of abuse to the land and its resources, but good treatment and inspiring aspects are not neglected. In contrast, one finds nothing except praise, pleasant descriptions, and appropriate anecdotes about American ecologists, many of whom became warm friends. Aldo Leopold was ". . . only fifty eight and his intellectual caliber was still increasing" (p. 84). As you talk with Olaus Murie ". . . his clarity of mind comes over to you and you understand things better in his presence" (p. 193). Paul Errington ". . . works in a rarefied atmosphere of thought, having come to it from extreme familiarity with one organism and its environmental complex. . ." (p. 200).

Darling seems too polite in avoiding sharp criticisms of practices and research of federal and state agencies concerned with conservation. One wishes for more stimulating comments such as those on page 219 concerning the large amount of overhead for small returns in research at the Coweeta Experimental Forest. Darling's thinking mind must be loaded with constructive suggestions that ought to be made available, however much they may hurt temporarily. One of the few contributions in this respect (p. 316) concerns the need for greater emphasis on vegetation studies in wildlife curricula.

There is so much of Darling's personal thought, habits, likes and dislikes, keen observation, sound biological interpretation, and beautiful writing in this book that one learns to know the man well. This provides an inspiration for all, and perhaps particularly for students and young biologists fresh on their first job.

For such a fast and large undertaking, there are remarkably few errors in fact and thought. This reviewer noted approximately a dozen, but they were so obviously inadvertent that they were not in the least distracting.

Darling's fresh view of the American scene is an extremely valuable contribution that will grace anyone's mind and book shelf. The Conservation Foundation chose wisely in sponsoring this worthy analysis of our country.

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JOSEPH WOOD KRUTCH'S DESERT[1]

Arizona and the desert does strange things to men. Some famed naturalists retire, there spend winters and dollars, and find that it passes time to drive forty miles to a cocktail party. Other famed non-naturalists retire there, and become naturalists. They strike root, joyously burst into flower, and develop fruits that add something new and vital to the nourishment of both intellect and spirit.

Joseph Wood Krutch is an ex-professor of dramatic literature who has attained renown and success for his contributions in the humanities. With an interest in the natural sciences that dates back to childhood times, he went to live in the desert outside Tucson, at the age of 58. Now, after five years, we hear this voice which repeatedly uses our word "ecology."

It is not the purpose of this review to stress the worth of this book as a naturalist's regional report. As such it is a valued addition to that literature, showing a remarkably sensitive comprehension, not only of the individual plants and animals, but of their integration into that phenomenon which is the desert. There are separate chapters on: climatology and geomorphology, the spadefoot toad and the roadrunner, the saguaro, the Cactaceae, the scorpion, the yucca and its moth, the kangaroo rat, naturalized species, adaptations to water shortage, altitudinal zonation, and sex. Unfortunately none of these words appear in the chapter titles! The Cactaceae masquerade as "How they got that way"; "And every single one of them is right" refers to the water shortage adaptations. Some publishers may think this device either cute, or literary; whereas I am sure many readers will find the enigma annoying on first reading, and exasperating when trying to relocate a discussion.

Throughout these pages the author shows a firm and more than adequate grasp of the scientific literature. Furthermore, he supplements this knowledge with simple but effective personal experiments. In my opinion by far the most significant component of these chapters is not their factual content, for that can be found in other books. It is not his style of writing, although that style is superior, clear, highly attractive, and studded with asides on human nature. Rather, the significance lies in his constant probing, questioning, and querying of matters truly in the realm of science, but which our contemporary scientific mores usually forbid us to think about, at least in full view of public gaze. In the century before Darwin it was customary to believe that everything in Nature was made by God, for the good of Man. It bothered a few that God would so effectively hide some needed things, but we were not troubled, too much. Scientific research was then a kind of find-the-Easter-egg game. The more recent technologic research has become an obsession to convert to man's "use" what his God had failed to make directly usable. Came the revolution of evolution, and a new dogma started its reign. One contemporary reality decrees that the phenomena of the biologic world are comprehensible in terms of conditioned reflexes and instinctive patterns of function and behavior, all related to evolutionary processes. This mechanistic and positivist philosophy is understandably dear to the hearts of scientists, because without it the universe becomes lawless unpredictable confusion, a situation our emotional nature will not tolerate. And for those who wish objectively to study our inherent subjectivity, there is a science of man. I do not wish to imply that Dr. Krutch, thinking within these frames, sets out to question the positivist dictum. Often however does he ask of the scientist "why?", "what for?". He gets an explanation, and then untactfully asks of us "But what will explain the explanation?" "Cause" and "purpose" constantly bother him. The actions of beasts seem manly, and those of men seem beastly—to the credit of both, it may be added. The resultant, after reading these chapters, is a healthy uncertainty, depending of course on the degree to which we have previously been needled with these ideas, and the degree to which our mechanistic hide is still prickable.

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[1] Krutch, Joseph Wood. 1955. The voice of the desert. 223 pp., illus. New York: William Sloane Associates. $3.75.

The penultimate chapter, "Conservation is not enough," will be to many the climax of the book. This was published originally in *The American Scholar,* and far transcends the desert in its scope. Man, he says, ". . . cannot keep indefinitely just one step ahead of overcrowding and starvation." But conservation, to Dr. Krutch, is only "enlightened selfishness." Even "The wisest . . . the most remotely long-seeing exploitation of resources is not enough. . . . In the end it will defeat itself and the earth will have been plundered no matter how scientifically and farseeingly the plundering has been done." Furthermore, "Neither man nor any other animal can afford to triumph in that struggle [for existence] too completely. . . To the victor belong the spoils in nature . . . , but for a time only. When there are no more spoils to be consumed, the victor dies." "Ultimately we may have to recognize that there is also a conflict between what is called the general good [of humanity] and a good still more general—the good . . . of the whole biological community." "Man is of all such creatures [in that community] one of those least able to stand alone." "To live healthily and successfully on the land we must also live with it." ". . . To some extent [therefore] the immediate interest of the human species may sometimes have to be disregarded." "How can he come to accept, not sullenly but gladly, the necessity of sharing the earth?" These thoughts, for all their massiveness, may be but a zephyr in a figurative wilderness. Today, as if in defiance of all such thoughts, we are being tossed ahead in an unprecedented outburst of exploding atoms, exploding human populations, and exploding economies, all synonymized and rationalized as the individual's right to a personal profit and to a high "standard of living." If there is an intelligence in the universe, ours must be to him an interesting, foolhardy, adventurous speculation.

Joseph Wood Krutch follows in the tradition of Thoreau and Aldo Leopold, both of whom he frequently quotes and for whom he has reverence and respect. It is in the last chapter, "The mystique of the desert," that he leaves science technology and conservation, and thus unfortunately the review limits for this type of journal. Building on Shavian metabiology, and not on the certain revelations of mystical cults, he passes on to speculative reason and to the realm of emotion. To the positivist scientist who changes his vestments on the holy day so as to worship, I recommend this chapter above all others. I also recommend it to the positivist who can remember that he once chose his science because of some mystical attachment to the rest of nature. That attachment, though atrophied by disuse, might yet be revived.

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DESERTS THE WORLD OVER[1]

When Buxton's account of the desert "fauna in relation to the environment" was originally published in 1923, it provided a valuable summary up to that time of conditions in deserts throughout much of the world. The book summarized some of the similarities and differences in desert life and desert climates in the Palearctic, Nearctic, Ethiopian, and Oriental regions. It emphasized the adaptations which enable animals to live in areas of extreme drought, heat, evaporation, and wind. Since 1923, so much more has been learned about the biota of our deserts and the responses of animals to desert conditions, especially here in North America, that many statements in Buxton's book, now reprinted but unchanged, seem far out-of-date. For example, the chapter (VII) on "The colours of desert animals" is sketchy by present standards and Buxton considers that the colors of desert animals, even though correlated with the colors of desert soils, are not necessarily protective or concealing from predators. Much additional information since Buxton's writing sheds additional light on this controversial matter of protective coloration. One can think of such papers as Dice and Blossom's[2] on the colors of our desert mammals, Benson's[3] and Hooper's[4] studies of rodents in gypsum sands and black lavas, and Dice's[5] important work on the effectiveness of protective coloration under minute illumination. Certainly the many recent papers such as these just mentioned would have been reviewed by Buxton and might have altered his conclusion about coloration in desert animals. Unfortunately, Buxton has no bibliography in the book and one does not know what works on various topics he has consulted.

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[1] Buxton, P. A. 1955. (Reprinting of 1923 ed.) Animal life in deserts: a study of the fauna in relation to the environment. xv + 176 pp., 43 figs. New York: St. Martin's Press. $4.25.

[2] Dice, L. R., & P. M. Blossom. 1937. Carnegie Inst. Wash. Pub. 485: 1-129.

[3] Benson, S. B. 1933. Univ. Calif. Publ. Zool., 40: 1-70.

[4] Hooper, E. T. 1941. Univ. Mich., Mus. Zool., Misc. Publ. Zool. 51: 1-47.

The reader will note that adaptive convergence in unrelated families of animals that live in widely separated deserts throughout the world, such as the kangaroo rats of North America, gerbils and jerboas of the Palearctic and Ethiopian regions, and some of the marsupial bandicoots of Australia, is paralleled by adaptive convergence in unrelated families of plants, such as the Cactaceae of North America and the Euphorbiaceae of South Africa. Buxton cites only one case known to him where small animals, in Palestine, are dependent upon a plant for moisture but not for food. In our own Southwest, bighorns during periods of extreme aridity "bark" the giant cactus or saguaro with their horns, liberating moisture not only for themselves but for many other animals.

This volume still serves as the main summary of desert life and conditions throughout the world even though it currently is incomplete and out-of-date for North America.

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[5] Dice, L. R. 1945. Amer. Nat. 79: 385-416.
———. 1947. Cont. Lab. Vert. Biol. 34: 1-20.

THE GEOCHEMISTRY OF WATER[1]

Any book about a scientific discipline which is written for the beginner or keen amateur is bound to evoke cries of dismay from the professionals; we all love our complexities so. Since Professor Kuenen cuts across several disciplines in this book, one may expect the cries to issue from many directions. While a number of the grievances will be merited, most will stem from the scientists' failure to remember the author's purpose as stated in the foreword. This is not meant to be a textbook.

Professor Kuenen, an eminent geologist and the author of a standard text in marine geology, has summarized the physical aspects of the geochemical cycle of water. He has wisely omitted the rôle of water in biological processes. Even with this large omission, the topics could not be treated exhaustively. The author's interests are reflected in the choice of emphasis in the book; large sections are concerned with water as an agent in geological processes. The material presented is well organized and written in a lively, colloquial manner. The translation into idiomatic English is exceedingly well done. Unfortunately, in the earlier chapters the author's attempts to translate the quantities involved in geochemical calculations into terms intelligible to the layman more often tend to overawe than to explain. Meterologists will take exception to his choice of theories on the fixation of nitrogen in the upper atmosphere, and some oceanographers will dislike his ideas on the formation of submarine canyons.

The many illustrations vary in quality from the excellent geological block diagrams to the Droodle on page 26. Some of the drawings are originally from the author's marine geology text, and do not quite fit the material they are used to illustrate in this book. On the whole, the illustrations are good. The plates are uniformly choice.

The organization of the book into separate chapters, each dealing with one of the several physical states of water, is a happy thought. While the author gives no critical bibliography (and indeed one would be out of place in a work of this nature), he has appended a selected list of references for further reading. Most of the titles are old familiar friends. Taken altogether, and allowing for the difference in aims, REALMS OF WATER is not up to the high level of Professor Kuenen's earlier MARINE GEOLOGY.

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[1] Kuenen, P. H. 1956. Realms of water: Some aspects of its cycle in nature. New York: John Wiley and Sons Inc. 327 pp., illus. + 16 plates. $6.50.

THE PRESERVATION OF INVERTEBRATES[1]

Ecologists who study animal communities have the problem of preserving a wide range of animal life. THE PRESERVATION OF NATURAL HISTORY SPECIMENS (Volume I—Invertebrates) edited and compiled by two British zoologists is a useful reference for such purposes as well as a guide for students. It is a compendium of standard techniques which have proved successful and for the most part have been published and are well known by those working in the respective groups. This work brings together in one volume the best and most recent methods recorded in biological literature supplemented by a few special methods developed especially for this book.

Special attention has been given to the selection of methods which give permanent preservation to the critical taxonomic features needed for identification. Items considered are narcotizing, killing, fixing, preserving, staining, mounting, pinning, stuffing, degreasing, relaxing, and storage for both immature and adult specimens. Marine, freshwater, and terrestrial forms are included. Fossils of some groups are also included. Each phylum of the animal kingdom and each class of the Arthropoda form the chapter headings. Nearly half of the text is devoted to the insect groups as would naturally be expected.

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[1] Wagstaffe, Reginald and J. Havelock Fidler. 1955. The preservation of natural history specimens. Volume 1, Invertebrates. xiii + 205 pp. New York: Philosophical Library. $10.00.

There is an appendix for: 1. apparatus and instruments (largely entomological); 2. reagents (with formulae for preparing fixing fluids, stains, narcotics, preservatives, dehydrating and cleaning agents, mounting media); 3. labels and labelling; 4. storage methods; and 5. microscopy. There are 139 line drawings, and a few references, largely British, are given at the end of each chapter. There is a complete index.

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CORRECTIONS

The following corrections should be made in the article by W. P. Lowry (ECOLOGY 37: 419-430. July, 1956).

p. 425: *First* parenthesis of Equation 7 should read $T_M + T_m/2)$ instead of $(T_M - T_m/2)$.

p. 428: Column 2, line 6, should read ". . . . expressed as *percentages* of the total area. . . ." instead of ". . . . expressed as *fractions*."

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